*Plate I.*

FIG. 1.

FIG. 2.

FIG. 1.—Human blood-corpuscles, fresh; magnified 840 diameters, $\frac{1}{18}$ inch homogeneous oi immersion-objective by Zeiss, original negative amplified twice (Stratford).

FIG. 2.—Blood of Guinea-pig, spread and dried on glass cover; magnified 1,450 diameters, 1 inch homogeneous oil-immersion-objective by Zeiss, and Tolles's amplifier (Sternberg).

# A TEXT-BOOK OF

# HUMAN PHYSIOLOGY



BY

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*WITH THREE HUNDRED AND SIXTEEN FIGURES IN THE TEXT, AND TWO PLATES*

FOURTH EDITION, ENTIRELY REWRITTEN





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# PREFACE.

THE present edition of this treatise has been rewritten; and while the general arrangement of subjects is retained, but little remains of the original text. Although the third edition, published in 1880, is still much used as a text-book, for several years I have not been able to follow it closely in public teaching; and its defects have become so important that it has seemed to me impossible to remedy them without making a new book.

I have thought it advisable to curtail still more the historical references contained in former editions. At the present day it is not possible to give even a brief account of the literature of physiology within the limits of a single volume of convenient size. I have avoided, also, as far as practicable, discussions of unsettled and disputed questions, as unprofitable and confusing.

I have adopted the new, chemical nomenclature, which is now almost universally accepted, but have not attempted to give a full account of the chemistry of the body. Physiological chemistry has now become a science by itself; and while it has contributed very largely to exact, physiological knowledge, its full consideration is properly confined to special treatises.

Recent advances in the knowledge of minute anatomy, due largely to improved instruments and methods, have had an important share in the progress of physiology. These have been considered incidentally, and they now form an essential part of all complete works on anatomy.

One who has long been a student and teacher of physiology can hardly fail to have an idea, more or less definite, of what a text-book should be, however imperfectly he may carry out this idea in his own work. I shall be more than satisfied if I have been able to give concise and connected statements of well-established facts, in such a form that they can easily be acquired by students and in language that can not be misunderstood. Peculiar views and theories, whether of the author or of others, have no proper place in a text-book, which should represent facts generally recognized and accepted, and not the ideas of any one individual

It does not seem to me that the value of a text-book is materially enhanced by elaborate descriptions of apparatus and methods, except as they involve principles susceptible of general, physiological application; nor does it seem profitable to follow out the details of intricate, mathematical calculations involved in certain studies, such as physiological optics and acoustics, the results of which are universally accepted. It is sufficient to teach by text-books the science of physiology. The art of investigation and the methods employed in physiological research are to be learned in the laboratory and from special treatises and monographs.

To those who, by early education and common usage, have long been accustomed to English weights and measures, the metric system frequently fails to convey a definite idea, without a mental reduction to the familiar standard; but the metric system is now very generally used in scientific works. In the text, the English weights and measures and the Fahrenheit scale of the thermometer have been retained, and their equivalents in the metric system are given in parentheses. In microscopic measurements the micromillimetre ($\frac{1}{1000}$ of a millimetre, or $\frac{1}{25000}$ of an inch), indicated by the Greek letter $\mu$, is frequently employed.

The form and typography of the book have been changed, it is hoped for the better. One new plate and sixty-one new figures have been introduced. Two plates and sixty-three figures have been discarded. The old illustrations which remain have been carefully examined and all remediable defects have been corrected. For most of the illustrations that have been retained, new electrotypes have been taken from the originals, and thirty cuts have been re-engraved. A few engravings, however, taken from classical authorities, though defective from an artistic point of view, have been retained in their original form. It is due to the publishers to make these statements, and to say that they have spared nothing in the mechanical execution of the work.

AUSTIN FLINT.

NEW YORK, *August*, *1888*.

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## CHAPTER I.

### *THE BLOOD.*

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WITH the progress of knowledge and the accumulation of facts in physiology, the importance of the blood in its relations to the phenomena of animal life becomes more and more thoroughly understood and appreciated. The blood is the most abundant and highly organized of the fluids of the body, providing materials for the regeneration of all parts, without exception, receiving the products of their waste and conveying them to proper organs, by which they are removed from the system. These processes require, on the one hand, constant regeneration of the nutritive constituents of the blood, and on the other, its constant purification by the removal of effete matters.

Those tissues in which the processes of nutrition are active are supplied with blood by vessels; but some, less highly organized, like the epidermis, hair, cartilage etc., which are called extra-vascular because they are not penetrated by vessels, are none the less dependent upon the blood, as they imbibe nutritive material from the blood of adjacent parts.

The importance of the blood in the processes of nutrition is evident; and in animals in which nutrition is active, death is the immediate result of its abstraction in large quantity. Its importance to life can be readily demonstrated by experiments upon the inferior animals. If, in a small dog, a canula adapted to a syringe be introduced through the right jugular vein into the right side of the heart, and a great part of the blood be suddenly withdrawn from the circulation, immediate suspension of all the so-called vital processes is the result; and if the blood be then returned to the system, the animal is as suddenly revived.

Certain conditions, one of which is diminution in the force of the heart's action after copious hæmorrhage, prevent the escape of all the blood from the body, even after division of the largest arteries; but after the arrest of the functions, which follows copious discharges of this fluid, life may be restored by injecting into the vessels the same blood or the fresh blood of another animal. This observation, which was first made on the inferior animals, has been applied to the human subject; and it has been ascertained that in patients sinking under hæmorrhage the introduction of even a few ounces of fresh blood may restore the functions for a time, and sometimes permanently.

*Quantity of Blood.*—The determination of the entire quantity of blood contained in the body has long engaged the attention of physiologists, without, however, any absolutely definite results. The fact that physiologists have not succeeded in determining definitely the entire quantity of blood shows the extent of the difficulties to be overcome before the question can be entirely settled. The chief difficulty lies in the fact that all the blood is not discharged from the body after division of the largest vessels, as after decapitation; and no perfectly accurate means have been devised for estimating the quantity which remains. The estimates of experimenters present the following wide differences: Allen-Moulins, who was one of the first to study this question, estimated the quantity of blood at one twentieth the weight of the entire body. The estimate of Herbst was a little higher. Hoffmann estimated the quantity at one fifth the weight of the body. These observers estimated the quantity remaining in the system after opening the vessels, by mere conjecture. Valentin was the first to attempt to overcome this difficulty by experiment. For this purpose he employed the following process: He took first a small quantity of blood from an animal for purposes of comparison; then he injected into the vessels a known quantity of a saline solution, and taking another specimen of blood some time after, he ascertained by evaporation the proportion of water which it contained, and compared it with the proportion in the first specimen. He reasoned that the excess of water in the second specimen over the first would give the proportion of the water which had been added to the whole mass of blood; and as the entire quantity of water introduced was known, the entire quantity of blood could be deduced therefrom.

The following process was employed by Lehmann and Weber, and was applied directly to the human subject in the cases of two decapitated criminals: These observers estimated the blood remaining in the body after decapitation, by injecting the vessels with water until it came through nearly colorless. The liquid was carefully collected, evaporated to dryness, and the dry residue was assumed to represent a certain quantity of blood, the proportion of dry residue in a definite quantity of blood having been previously ascertained. If it were certain that only the solid matter of the blood was thus removed, such an estimate would be tolerably accurate.

The process just described gives an idea of the probable quantity of blood in the body; but the most serious objection to it is the possibility that certain solid constituents of the tissues are washed out by the water passing through the vessels, and it is generally thought that the estimate by Lehmann and Weber, that the quantity of blood is equal to about one eighth of the weight of the body, is too high. More recent observations have been made upon the inferior animals, by various methods, which are all more or less open to objection, and which it is not necessary to describe in detail; but the results of nearly all of the experiments made within the last few years show a less proportion of blood than was estimated by Lehmann and Weber. Remembering that all estimates must be regarded as approximate, it may be assumed that in a person of ordinary adipose and muscular development the proportion of blood to the weight of the body is about one to ten. The relative quantity of blood is less in the infant than in the adult and is diminished in old age. It has been found, also, in observations on the inferior animals, to be greater in the male than in the female.

Prolonged abstinence from food, except when large quantities of liquid are ingested, has a notable effect in diminishing the mass of blood, as indicated by the small quantity which can be removed from the body, under this condition, with impunity; and it has been experimentally demonstrated that the entire quantity of blood is considerably increased during digestion. Bernard drew from a rabbit weighing about two and a half pounds (1,134 grammes), during digestion, ten and a half ounces of blood (300 grammes) without producing death; while he found that the removal of half that quantity from an animal of the same size, fasting, was fatal. Wrisberg reported a case of a female criminal, very plethoric, from whom nearly twenty-one and a half pounds of blood (9,745 grammes) flowed after decapitation. As the relations of the quantity of blood to digestion are so important, it is unfortunate that the conditions in this respect were not noted in the observations of Lehmann and Weber. It is evident that the quantity of blood in the body must be considerably increased during digestion; but as regards the extent of this increase, it is not possible to form any very definite idea. It is shown only that there is a marked difference in the effects of hæmorrhage in animals during digestion and fasting.

## General Characters of the Blood.

*Opacity.*—The opacity of the blood depends upon the fact that it is not a homogeneous fluid, but is composed of two distinct elements, a clear plasma and corpuscles, which are both nearly transparent but which have each a different refractive power. If both of these elements had the same refractive power, the mixture would present no obstacle to the passage of light; but as it is, the rays, which are refracted in passing from the air to the plasma, are again refracted when they enter the corpuscles, and again, when they pass from the corpuscles to the plasma, so that they are lost, even in a thin layer of the fluid.

*Odor, Taste, Reaction and Specific Gravity.*—The blood has a faint but characteristic odor. This may be developed so as to be very distinct, by the addition of a few drops of sulphuric acid, when an odor peculiar to the animal from which the blood has been taken becomes very marked.

The taste of the blood is faintly saline, on account of the presence of a considerable proportion, three or four parts per thousand, of sodium chloride in the plasma.

The reaction of the blood is always distinctly alkaline. It is not easy, however, to demonstrate the alkalinity of the blood, on account of the red color of the blood-corpuscles; but the difficulty may be avoided by using certain precautions. The following method, employed by Schäfer, is quite satisfactory: A drop of blood is put upon a piece of glazed, reddened litmus-paper. After a few seconds the blood is lightly wiped off with a damp cloth, leaving a spot of a distinctly blue color. According to Zuntz, the alkalinity diminishes rapidly after the blood is drawn from the vessels. The alkaline reaction is due to the presence of sodium carbonate and sodium phosphate in the plasma.

The specific gravity of defibrinated blood is between 1052 and 1057 (Robin), being somewhat less in the female than in the male. The density varies greatly under different conditions of digestion.

*Temperature.*—The temperature of the blood is generally given as between 98° and 100° Fahr. (36·67° and 37·78° C.); but experiments have shown that it varies considerably in different parts of the circulatory system, independently of exposure to the refrigerating influence of the atmosphere. By the use of very delicate registering thermometers, Bernard succeeded in establishing the following facts with regard to the temperature in various parts of the circulatory system, in dogs and sheep:

1. The blood is warmer in the right than in the left cavities of the heart.
2. It is warmer in the arteries than in the veins, with a few exceptions.
3. It is generally warmer in the portal vein than in the abdominal aorta, independently of the digestive act.
4. It is constantly warmer in the hepatic than in the portal veins.

He found the highest temperature in the blood of the hepatic vein, where it ranged between 101° and 107° Fahr. (38·33° and 41·67° C.). In the aorta, it ranged between 99° and 105° Fahr. (37·22° and 40·55° C.). It may be assumed, then, in general terms, that the temperature of the blood in the deeper vessels is between 100° and 107° Fahr. (37·78° and 41·67° C.).

*Color.*—The color of the blood is due to the corpuscles. In the arterial system it is uniformly red. In the veins it is generally dark blue and sometimes almost black. The color in the veins, however, is not constant. Many years ago, John Hunter observed, in a case of syncope, that the blood drawn by venesection was bright red; and more recently, Bernard has demonstrated that in some veins, the blood is nearly if not quite as red as in the arterial system. The color of the venous blood depends upon the condition of the organ or part from which it is returned. The red color was first noticed by Bernard in the renal veins, where it contrasts very strongly with the black blood in the vena cava. He afterward observed that the redness existed only during the activity of the kidneys; and when, from any cause, the secretion of urine was arrested, the blood became dark. He was led, from this observation, to examine the venous blood from other glands; and directing his attention to those which he was able to examine during their activity, particularly the salivary glands, he found the blood red in the veins during secretion, but becoming dark as soon as secretion was arrested. In the submaxillary gland, by Faradization of a certain nerve, called the motor nerve of the gland, Bernard was able to produce secretion, and by stimulating another nerve, to arrest it; in this way changing at will the color of the blood in the vein. It was found by the same observer that division of the sympathetic in the neck, which dilates the vessels and increases the supply of blood to one side of the head, produced a red color of the blood in the jugular. He also found that paralysis of a member by division of the nerve had the same effect on the blood returning by the veins.

The explanation of these facts is evident in view of the reasons why the blood is red in the arteries and dark in the veins. Its red color depends upon the presence of oxygen in the corpuscles; and as the blood passes through the lungs it loses carbon dioxide and the corpuscles gain oxygen, changing from black to red. In its passage through the capillaries of the system, in the ordinary processes of nutrition, the blood loses oxygen and gains carbon dioxide, changing from red to black. During the intervals of secretion, the glands receive just enough blood for their nutrition, and the ordinary interchange of gases takes place, with the consequent change of color; but during secretion, the blood is supplied to the glands in greatly increased quantity. Under these conditions, it does not lose oxygen and gain carbon dioxide in any great quantity, as has been demonstrated by actual analysis, and consequently there is no marked change in color. When filaments of the sympathetic are divided, the blood-vessels are dilated, and the supply of blood is increased to such an extent that a certain proportion passes through without parting with its oxygen—a fact which has also been demonstrated by analysis—and consequently it retains its red color. The explanation in cases of syncope is probably the same, although this is merely a supposition, Even during secretion, a certain quantity of carbon dioxide is formed in the gland, which, according to Bernard, is carried off in solution in the secreted fluid.

It may be stated, then, in general terms, that the color of the blood in the arteries is bright red; and in the ordinary veins, like the cutaneous or muscular, it is dark blue, almost black. It is red in the veins coming from glands during secretion, and dark during the intervals of secretion.

### Anatomical Elements in the Blood.

In 1661, Malpighi, in examining the blood of the hedgehog, with the imperfect lenses at his command, discovered little floating particles which he mistook for granules of fat, but which were the blood-corpuscles. He did not extend his observations in this direction; but a few years later (1673), Leeuwenhoek, by the aid of simple lenses of his own construction, ranging in magnifying power between forty and one hundred and sixty diameters, first saw the corpuscles of human blood, which he minutely described in a paper published in the Philosophical Transactions, in 1674. To Leeuwenhoek is generally ascribed the honor of the discovery of the blood-corpuscles. About a century later, William Hewson described another kind of corpuscles in the blood, much less abundant than the red, which are now known under the name of white globules, or leucocytes.

Without following the progress of microscopical investigations into the constitution of the blood, it may be stated that it is now known to be composed of a clear fluid, the plasma, or liquor sanguinis, holding certain corpuscles in suspension. These corpuscles are of three kinds:

1. Red corpuscles; by far the most abundant, constituting a little less than one-half of the mass of blood.

2. Leucocytes, or white corpuscles; much less abundant, existing only in the proportion of 1 to 750 or 1,000 red corpuscles.

3. Blood-plaques; varying in size, shape and number.

*Red Corpuscles.*—These little bodies give to the blood its red color and its opacity. They are organized structures, containing organic nitrogenized and inorganic matters molecularly united and a little fatty matter in union with the organic constituents. They constitute a little less than one-half the mass of blood, and according to the observations of all who have investigated this subject, are more abundant in the male than in the female.

FIG. 1.—*Human blood-corpuscles; magnified* 1,450 *diameters* (Sternberg).
This figure also shows a leucocyte containing four fatty granules.

The form of the blood-corpuscles is peculiar. They are flattened, biconcave, circular disks, with a thickness of one-fourth to one-third of their diameter. Their edges are rounded, and the thin, central portion occupies about one-half of their diameter. Their consistence is not much greater than that of the plasma. They are very elastic, and if deformed by pressure, immediately resume their original shape when the pressure is removed. Their specific gravity is between 1088 and 1105, considerably greater than the specific gravity of the plasma, which is about 1028.

When the blood has been drawn from the vessels and coagulates slowly, the greater density of the red corpuscles causes them to gravitate to the lower portions of the clot, leaving the white corpuscles and fibrin at the surface. If coagulation be prevented by the addition of a small quantity of sodium sulphate, there is quite a marked gravitation of red corpuscles after standing for some hours.

The peculiar form of the blood-corpuscles gives them a very characteristic appearance under the microscope. Examined with a magnifying power of between three hundred and five hundred diameters, those which present their flat surfaces have a shaded centre when the edges are exactly in focus.

This appearance is an optical effect due to the form of the corpuscles; their biconcavity rendering it impossible for the centre and edges to be exactly in focus at the same instant, so that when the edges are in focus, the centre is dark, and when the centre is bright, the edges are shaded.

As the blood-corpuscles are examined with the microscope, by transmitted light, they are nearly transparent and of a pale-amber color. It is only when they are collected in masses that they present the red tint characteristic of blood as it appears to the naked eye. This yellow or amber tint is quite characteristic. An idea of the color may be obtained by largely diluting blood in a test-tube and holding it between the eye and the light.

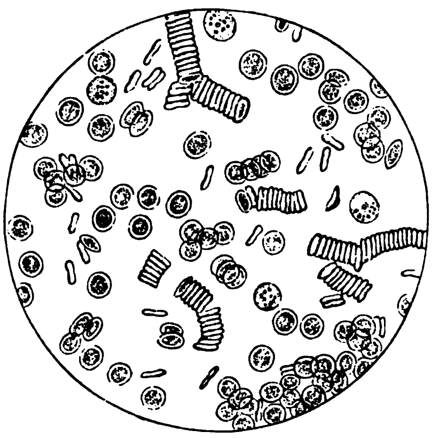

FIG. 2.—*Human red blood-corpuscles, arranged in rows* (Funke).

In examining blood under the microscope, the corpuscles are seen in many different positions, and this assists in the recognition of their peculiar form.

It has long been observed that the blood-corpuscles have a remarkable tendency to arrange themselves in rows like *rouleaux* of coin. This appearance is due to the following conditions:

Shortly after removal from the vessels, there exudes from the corpuscles an adhesive substance which causes them to stick together. Of course the tendency is to adhere by their flat surfaces (Robin). This phenomenon is due to a post-mortem change; but it occurs so soon, that it presents itself in nearly every specimen of fresh blood, and is therefore mentioned in connection with the normal characters of the blood-corpuscles.

The diameter of the blood-corpuscles has a more than ordinary anatomical interest; for, varying perhaps less in size than other anatomical elements, they are often taken as the standard by which an idea is formed of the size of other microscopic objects. The diameter usually given is $\frac{1}{3500}$ of an inch (7·17 $\mu$). The exact measurement given by Robin is $\frac{1}{3437}$ of an inch (7·3 $\mu$). Very few corpuscles are to be found which vary from this measurement. Kölliker, who gives their average diameter as $\frac{1}{3600}$ of an inch (7 $\mu$), states that "at least ninety-five out of every hundred corpuscles are of the same size."

Measurements of the blood-corpuscles of different animals are important, from the fact that it often becomes a question to determine whether a given specimen of blood be from the human subject or from one of the inferior animals. Comparative measurements also have an interest on account of a relation which seems to exist in the animal scale between the size of the blood-corpuscles and muscular activity. In all the mammalia, with the exception of the camel and llama, in which the corpuscles are oval, the blood has nearly the same anatomical characters as in the human subject. In only two animals, the elephant and sloth, are the red corpuscles larger than in man; and in all others, they are smaller or of nearly the same diameter. In some animals, the corpuscles are very much smaller than in man, and by accurate measurements, their blood can be distinguished from the blood of the human subject; but in forming an opinion on this subject, it must be remembered that there is some variation in the size of the corpuscles of the same animal. The blood of the human subject or of the mammals generally can be readily distinguished from the blood of birds, fishes or reptiles; for in these animals, the corpuscles are oval and contain a granular nucleus.

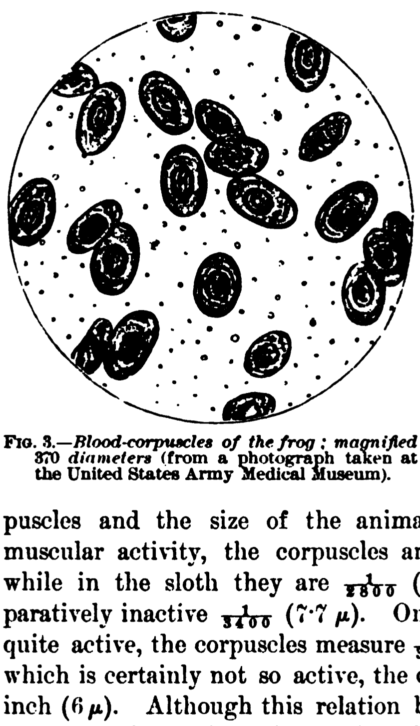

FIG. 3.—*Blood-corpuscles of the frog; magnified 370 diameters* (from a photograph taken at the United States Army Medical Museum).

Milne-Edwards has attempted to show, by a comparison of the diameter of the blood-corpuscles in different species, that their size bears an inverse ratio to the muscular activity of the animal. This relation holds good to some extent, while there certainly exists none between the size of the corpuscles and the size of the animal. In deer, animals remarkable for muscular activity, the corpuscles are very small, $\frac{1}{5000}$ of an inch (5 $\mu$); while in the sloth they are $\frac{1}{2800}$ (8·9 $\mu$), and in the ape, which is comparatively inactive $\frac{1}{3400}$ (7·7 $\mu$). On the other hand, in the dog, which is quite active, the corpuscles measure $\frac{1}{3500}$ of an inch (7·17 $\mu$), and in the ox, which is certainly not so active, the diameter of the corpuscles is $\frac{1}{4200}$ of an inch (6 $\mu$). Although this relation between the size of the blood-corpuscles and muscular activity is not invariable, it is certain that, the higher the animal in the scale, the smaller are the blood-corpuscles; the largest being found in the lowest orders of reptiles, and the smallest, in the mammalia. The blood of the invertebrates, with a few exceptions, contains no colored corpuscles.

*Enumeration of the Blood-Corpuscles.*—In most of the quantitative analyses of the blood, the proportion of moist corpuscles to the entire mass of blood is stated to be a little less than one-half. This estimate is necessarily rather rough; and it would be useful to ascertain, if possible, the normal variations in the proportion of corpuscles, under different conditions of the system, particularly as these bodies play so important a part in many of the functions of the organism. Actual enumerations of the blood-corpuscles have been made by Vierordt, Weckler, Malassez and others. It is stated by Malassez that the error in his calculations is not more than two or three per cent. The process employed by Malassez is the following:

The blood to be examined is diluted with ninety-nine parts of a liquid composed of one volume of a solution of gum-arabic of a specific gravity of 1020 with three volumes of a solution of equal parts of sodium sulphate and of sodium chloride, also of a specific gravity of 1020. The mixture, containing one part of blood in one hundred, is introduced into a small thermometer-tube with an elliptical bore, the sides of the tube being ground flat for convenience of microscopical examination. The capacity of the tube is to be calculated by estimating the weight of a volume of mercury contained in a given length. The tube is then filled with the diluted blood, and the number of corpuscles in a given length of the tube is counted by means of a microscope fitted with an eye-piece micrometer. In this way, the number of corpuscles in a given volume of blood can be readily estimated. In man, the number in a cubic millimetre of blood—a millimetre = about $\frac{1}{25}$ of an inch—is estimated to be between four and a half and five millions.

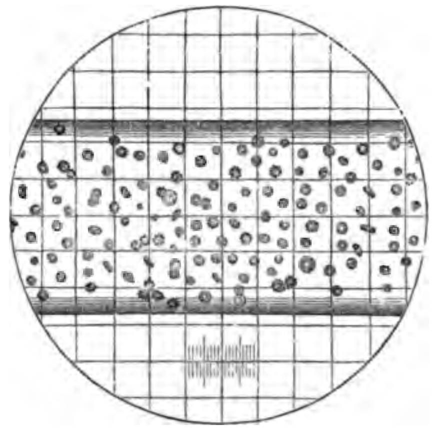

FIG. 4.—*Artificial capillary, filled with a sanguineous mixture, seen under a quadrilateral micrometer* (Malassez).

According to the observations of Malassez, the proportion of corpuscles is about the same in all parts of the arterial system. In the veins, the corpuscles are more abundant than in the arteries. In the venous system, the blood of the splenic veins presents the largest proportion of corpuscles, and the proportion is smallest in the blood of the hepatic veins. These results favor the idea that the red corpuscles are formed, to a certain extent, in the spleen and that some are destroyed in the liver; but farther observations are necessary to render this view certain.

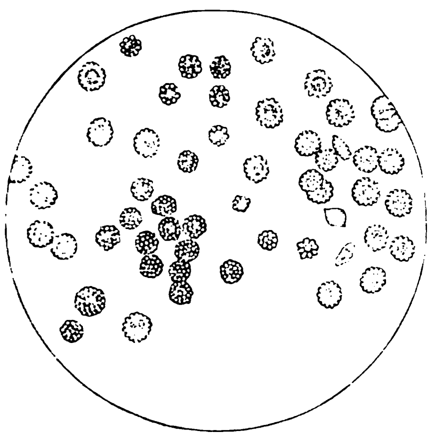

FIG. 5.—*Human blood-corpuscles, showing post-mortem alterations* (Funke).

*Post-mortem Changes in the Blood-Corpuscles.* — In examining the fresh blood under the microscope, after the specimen has been under observation a short time, the corpuscles are observed to assume a peculiar appearance, from the development, on their surface, of very minute, rounded projections, like the granules of a raspberry. A little later, when they have become partly desiccated, they present a shrunken appearance and their edges are more or less serrated. Under these conditions, their original form may be restored by adding to the specimen a liquid of about the density of the serum. When they have been completely dried, as in blood spilled upon clothing or on a floor, they can be made to assume their characteristic form by carefully moistening them with an appropriate liquid. This property is taken advantage of in examinations of old spots supposed to be blood; and if the manipulations be carefully conducted, the corpuscles may be recognized without difficulty by means of the microscope.

If pure water be added to a specimen of blood under the microscope, the corpuscles swell up, become spherical and are finally dissolved. The same effect follows almost instantaneously on the addition of acetic acid.

*Structure.*—The blood-corpuscles are perfectly homogeneous, presenting, in their normal condition, no nuclei or granules, and are not provided with an investing membrane. The appearances presented upon the addition of iodine to blood previously treated with water, which have been supposed to indicate the presence of shreds of ruptured vesicles, are not sufficiently distinct to demonstrate the existence of a membrane. The great elasticity of the corpuscles, the persistence with which they preserve their biconcave form, and their general appearance, rather favor the idea that they are homogeneous bodies of a definite shape, than that they have a cell-wall with semi-fluid contents; especially as the existence of a membrane has been only inferred and not positively demonstrated.

*Development of the Blood-Corpuscles.*—Very early in the development of the ovum, the blood-vessels appear, constituting what is called the area vasculosa. At about the same time, the blood-corpuscles are developed, it may be before, or it may be just after the appearance of the vessels, for this point is undetermined. The blood becomes red when the embryon is about one-tenth of an inch (2·5 mm.) in length. From this time until the end of the sixth or eighth week, they are thirty to one hundred per cent. larger than in the adult. Most of them are circular, but some are ovoid and a few are globular. At this time, nearly all of them are provided with a nucleus; but from the first, there are some in which this is wanting. The nucleus is $\frac{1}{8000}$ to $\frac{1}{7000}$ of an inch (3·1 $\mu$ to 3·6 $\mu$) in diameter, globular, granular and insoluble in water and acetic acid. As development advances, these nucleated corpuscles are gradually lost; but even at the fourth month, a few remain. After this time, they do not differ anatomically from the blood-corpuscles in the adult.

In many works on physiology and general anatomy, accounts are given of the development of the red corpuscles from the colorless corpuscles, or leucocytes, which are supposed to become disintegrated, their particles becoming developed into red corpuscles; but there seems to be no positive evidence that such a process takes place. The red corpuscles appear before the leucocytes are formed; and it is mainly the fact that the two varieties coexist in the blood-vessels which has given rise to such a theory. It is most reasonable to consider that the first red corpuscles are formed in the area vasculosa in the same way that other anatomical elements make their appearance at that time, the exact process not being understood. In the later periods of development of the fœtus and in the adult, it is probable that the red marrow of the bones and, perhaps, to a certain extent, the spleen have important uses in connection with the development of the red blood-corpuscles. The observations of Neumann, of Königsburg, and of Bizzozero, of Turin, about the year 1868, have been extended and confirmed by others, and show that there is a generation of red corpuscles in the red marrow of the bones, which is now regarded as the most important of the so-called corpuscle-forming organs. In the fœtus and in the young infant, the marrow of nearly all the bones is red, or of the kind called lymphoid. In the adult, the marrow of the long bones is yellow, or fatty, the red marrow being confined to the cancellated structure of the short and the flat bones. Although the researches with regard to the spleen are less positive and definite in their results, it is probable that this organ also contributes to the development of the red blood-corpuscles.

The exact mode of development of the red corpuscles in the marrow and in the spleen has not been very satisfactorily described and is still a question concerning which there is much difference of opinion among histologists. A full discussion of this question would be out of place in this work, which is intended to embrace only those points in histology that have been definitely settled.

It is probable that the red corpuscles are, in certain number, destroyed in the passage of the blood through the liver and perhaps, also, in the spleen, the coloring matter contributing to the formation of the biliary and the urinary pigmentary matters. If this view be accepted, the spleen is concerned in both the formation and the disintegration of blood-corpuscles.

In the present state of knowledge, the following seem to be the most rational views with regard to the development and destination of the red blood-corpuscles.

1. At the time of their first appearance in the ovum, the blood-corpuscles are formed by no special organs, for no special organs then exist.

2. In the fœtus, after the development of the marrow of the bones and of the spleen, and in the adult, these parts have important uses in the formation of the red corpuscles, especially the red marrow of the bones.

3. It is probable that the red blood-corpuscles are constantly undergoing destruction, and that their coloring matter contributes to the formation of other pigmentary matters. As the corpuscles are thus destroyed, and as they are diminished in number in disease or by hæmorrhage, they are probably replaced by new corpuscles formed in greatest part in the red marrow of the bones.

4. Pathological observations seem to show that in certain cases of anæmia, when there is an abnormal destruction of red corpuscles, the activity of the corpuscle-forming office of the marrow is increased, compensating, to a certain extent, the conditions which involve the abnormal destruction of the corpuscles.

*Uses of the Red Blood-Corpuscles.*—Although the albuminoid constituents of the plasma of the blood are essential to nutrition, the red corpuscles are the parts most immediately necessary to life. It is well known that life may be restored to an animal in which the functions have been suspended by hæmorrhage, by the introduction of fresh blood; and while it is not necessary that this blood should contain the fibrin-factors, it has been shown by the experiments of Prévost and Dumas and others, that the introduction of serum, without the corpuscles, has no permanent restorative effect. When all the arteries leading to a part are tied, the tissues lose their properties of contractility, sensibility etc., which may be restored, however, by supplying it again with blood. It will be seen, in treating of respiration, that one great distinction between the corpuscular and fluid elements of the blood is the great capacity which the former have for absorbing gases. Direct observations have shown that blood will absorb ten to thirteen times as much oxygen as an equal bulk of water; and this is dependent almost entirely on the presence of the red corpuscles. As all the tissues are constantly absorbing oxygen and giving off carbon dioxide, a very important office of the corpuscles is to carry oxygen to all parts of the body. In the present state of knowledge, this is the only well-defined use which can be attributed to the red corpuscles, and it undoubtedly is the principal one. They have an affinity, though not so great, for carbon dioxide which, after the blood has circulated in the capillaries of the system, takes the place of the oxygen. In a series of experiments on the effects of hæmorrhage and the seat of the "sense of want of air," it was demonstrated that one of the results of removal of blood from the system was a condition of asphyxia, dependent upon the absence of these respiratory elements (Flint, 1861).

*Leucocytes, or White Corpuscles of the Blood.*—In addition to the red corpuscles of the blood, this fluid always contains a number of colorless bodies, globular in form, in the substance of which are embedded a greater or less number of minute granules, forming a nucleus of irregular shape. These have been called by Robin, leucocytes. This name seems more appropriate than that of white or colorless blood-corpuscles, inasmuch as these bodies are not peculiar to the blood, but are found in the lymph, chyle, pus and various other fluids, in which they were formerly known by different names. The description which will be given of the white corpuscles of the blood, and the effects of reagents, will answer, in the main, for all the corpuscular bodies that are grouped together under the name of leucocytes.

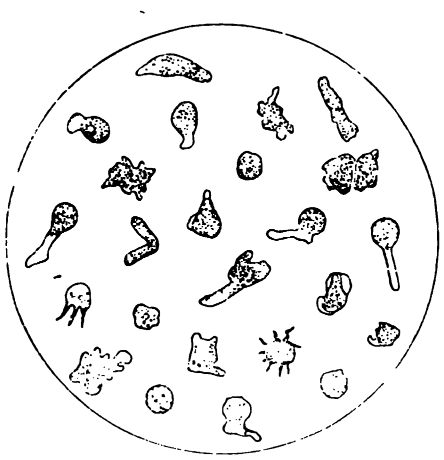

FIG. 6.—*Human leucocytes, showing amœboid movements* (Landois).

Leucocytes are normally found in the blood, lymph, chyle, semen, colostrum and vitreous humor. Pathologically, they are found in the secretion of mucous membranes, following irritation, and in inflammatory products, when they are called pus-corpuscles. They are globular, with a smooth surface, somewhat opaque from the presence of more or less granular matter, white, and larger than the red corpuscles. In examining the circulation under the microscope, the adhesive character of the leucocytes as compared with the red corpuscles is readily noted. The latter circulate with great rapidity in the centre of the vessels, while the leucocytes have a tendency to adhere to the sides, moving along slowly, and occasionally remaining stationary for a time, until they are swept along by a change in the direction or force of the current.

The size of the leucocytes varies somewhat, even in any one fluid, such as the blood. Their average diameter may be stated as $\frac{1}{2500}$ of an inch (10 $\mu$). It is in pus, where they exist in greatest abundance, that their microscopical characters may be studied with most advantage. In this fluid, after it is discharged, the corpuscles sometimes present remarkable changes in form. They become polygonal in shape, and sometimes ovoid, occasionally presenting projections from their surface, which give them a stellate appearance. These alterations, however, are only temporary; and after twelve to twenty-four hours, they resume their globular shape. On the addition of acetic acid they swell up, become transparent, with a delicate outline, and present in their interior one, two, three or even four rounded, nuclear bodies, generally collected in a mass. This appearance is produced, though more slowly, by the addition of water. In some corpuscles a nucleus may be seen without the addition of any reagent.

Leucocytes vary considerably in their external characters in different situations. Sometimes they are very pale and almost without granulations, and sometimes they are filled with fatty granules and are not rendered clear by acetic acid. As a rule, they increase in size and become granular when confined in the tissues. In colostrum, where they are called colostrum-corpuscles, they generally undergo this change. As the result of inflammatory action, when they are sometimes called inflammatory or exudation-corpuscles, leucocytes frequently become much hypertrophied and are filled with fatty granules.

The deformation of the leucocytes to which allusion has already been made is sometimes so rapid and changeable as to produce creeping movements, due to the projection and retraction of portions of their substance. These movements are of the kind called amœboid and are supposed to be important in the process of migration of the corpuscles.

The relative number of leucocytes, can only be given approximately. It has been estimated by counting under the microscope the red corpuscles and leucocytes contained in a certain space. The average proportion in man is probably 1 to 750 or 1000. It has been found by Hirt, whose observations have been confirmed by others, that the relative quantity of leucocytes is much increased during digestion. He found, in one individual, a proportion of 1 to 1800 before breakfast; an hour after breakfast, which was taken at 8 o'clock, 1 to 700; between 11 and 1 o'clock, 1 to 1500; after dining, at 1 o'clock, 1 to 400; two hours after, 1 to 1475; after supper, at 8 P. M., 1 to 550; at 11½ P. M., 1 to 1200. The leucocytes are much lighter than the red corpuscles, and when the blood coagulates slowly, they are frequently found, with a certain quantity of colorless fibrin, forming a whitish layer on the surface of the clot. Their specific gravity is about 1070.

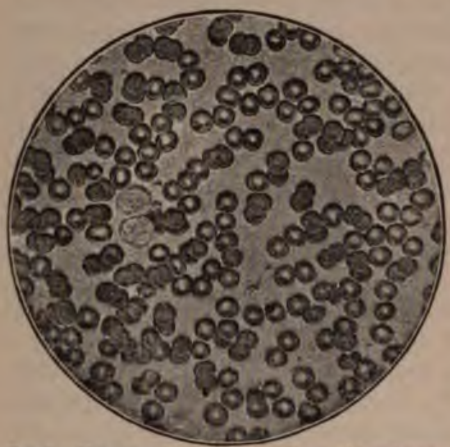

FIG. 7.—*Human red blood-corpuscles and two leucocytes* (Sternberg).

*Development of Leucocytes.*—These corpuscles appear in the blood-vessels very early in fœtal life, before the lymphatics can be demonstrated. They appear in lymphatics before these vessels pass through the lymphatic glands, in the fœtus anterior to the development of the spleen, and also on the surface of mucous membranes; so that they can not be considered as produced exclusively by the lymphatic glands, as has been supposed. Although they frequently appear as a result of inflammation, this process is by no means necessary for their production. Robin has observed the phenomena of their development in recent wounds. The first exudation consists of clear fluid, with a few red corpuscles. There appears afterward, a finely granular blastema. In a quarter of an hour to an hour, pale, transparent globules, $\frac{1}{8000}$ to $\frac{1}{6000}$ of an inch (3 $\mu$ to 4 $\mu$) in diameter, make their appearance, which soon become finely granular and present the ordinary appearance of leucocytes.

Histological researches show that in the adult, the number of leucocytes in the lymph is increased during the passage of this fluid through the lymphatic glands. The blood, also, in passing through the spleen has been shown to gain largely in these corpuscles. These facts are important in connection with the pathology of leucocythæmia. This disease, which is characterized by an excess of leucocytes in the blood, is now generally regarded as having a close relation to certain changes in the spleen, the lymphatic glands and the marrow of the bones. There is, indeed, a variety of the disease, known as lymphatico-splenic leucocythæmia, in which the spleen and certain of the lymphatic glands are enlarged, and another form, called medullo-lymphatic leucocythæmia, in which changes have been noted in the lymphatic glands and in the marrow. The anatomical changes which have been observed in the spleen, lymphatic glands and marrow, in leucocythæmia, are largely hyperplastic; that is, the normal structure of these parts is increased in extent. On the other hand, a disease called pseudo-leucocythæmia, presenting the anatomical characters and general symptoms of leucocythæmia, without an increase in the leucocytes of the blood, has been accurately described. Pathological observations, therefore, are not entirely in accord with the theory that the spleen, lymphatic glands and the bone-marrow are always directly concerned in the production of leucocytes.

Taking into consideration the histological and pathological observations bearing on the question, the following seems to be the most reasonable view with regard to the mode of development of leucocytes:

1. In early fœtal life the leucocytes of the blood are developed without the intervention of any special organs, and perhaps, also, these bodies are multiplied by division.

2. In adult life the same processes of development probably occur in the blood and lymph and in other situations.

3. It is probable, though by no means certain, that the spleen, lymphatic glands and the red marrow of the bones are more or less actively concerned in the production of leucocytes, both under physiological and pathological conditions; but it is certain that these organs and parts are not the exclusive seat of development of the so-called white blood-corpuscles and lymph-corpuscles.

*Uses of the Leucocytes.*—It is impossible, in the present state of physiological knowledge, to assign any definite use to the leucocytes of the blood and lymph. These bodies may be concerned to some extent in the development of the red blood-corpuscles, but this view, which is held by many physiologists, has no absolutely positive basis in fact. All that can be said is that the office of the leucocytes has not been ascertained. Their action, however, is important in the process of coagulation of the blood, lymph and chyle.

*Blood-Plaques.*—The so-called blood-plaques, described quite elaborately by Bizzozero and others, have been long known to histologists, under a variety of names, such as globulins, elementary corpuscles, granular *débris*, granule masses, hæmatoblasts etc. Until within a few years these bodies have not been thought to be of much importance, and even now little is known of their physiological and pathological relations.

The blood-plaques in human blood may be easily observed, preparing the blood by the following method (Osler):

"Upon the thoroughly cleansed finger-pad a single drop of the solution is placed, and with a sharp needle, or pricker, the skin is pierced through the drop, so that the blood passes at once into the fluid, which is then received upon a slide and covered. The withdrawal of the corpuscles into the solution prevents the plaques from aggregating, and they remain as isolated and distinct elements. The amount of blood allowed to flow into the drop must not be large, and should be quickly mixed. In many respects the most suitable medium is osmic acid, one-half to one per cent., which has the advantage that by its use permanent preparations can be obtained."

The plaques are thin, circular discs, homogeneous or very faintly granular and of a pale, grayish tint. They measure $\frac{1}{17000}$ to $\frac{1}{10000}$ (1·5 to 2·5 $\mu$) in diameter, about one-sixth of the diameter of the red blood-corpuscles. They exist in the blood in the proportion of one to about eighteen or twenty red corpuscles.

In the circulating blood, the plaques are distinct; but when the blood is drawn from the vessels, they adhere together and are usually collected into masses. The plaques quickly undergo change out of the body, becoming

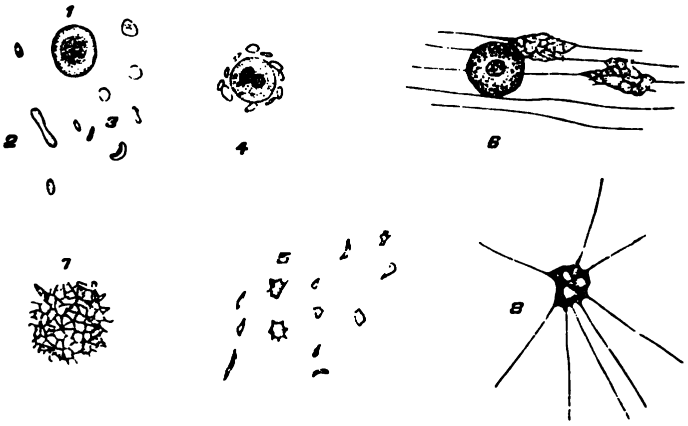


FIG. 8.—*Blood-plaques and their derivatives, partly after Bizzozero and Laker* (Landois).
1, red blood-corpuscles on the flat; 2, from the side; 3, unchanged blood-plaques; 4, a lymph-corpuscle surrounded with blood-plaques; 5, blood-plaques variously altered; 6, a lymph-corpuscle with two masses of fused blood-plaques and threads of fibrin; 7, group of blood-plaques fused or run together; 8, a similar small mass of partially dissolved blood-plaques with fibrils of fibrin.

ovoid, elongated or pointed. They sometimes send out processes which give them a stellate appearance.

Physiologists have no knowledge of the uses of the blood-plaques. The relations which have been supposed to exist between these bodies and the development of the other corpuscular elements of the blood, the phenomena of coagulation, etc., are as yet indefinite and uncertain.

## Composition of the Blood-Corpuscles.

The red corpuscles of the blood contain an organic nitrogenized substance, called globuline, combined with inorganic salts and a coloring matter. The composition of the leucocytes has not been accurately determined, and nothing is known of the composition of the blood-plaques. The inorganic matters contained in the red corpuscles are in a condition of intimate union with the other constituents, and can be separated only by incineration. It may be stated, in general terms, that most, if not all of the various inorganic constituents of the plasma exist also in the corpuscles, which latter are particularly rich in the salts of potassium. Iron exists in the coloring matter of the corpuscles. In addition, the corpuscles contain cholesterine, lecethine, a certain quantity of fatty matter and probably some of the organic saline constituents of the blood.

*Globuline.*—Rollett, by alternately freezing and thawing blood several times in succession in a platinum vessel, has succeeded in separating the coloring matter from the red corpuscles. When the blood is afterward warmed and liquefied, the fluid is no longer opaque but is dark and transparent. Microscopical examination then reveals the corpuscles, entirely decolorized and floating in a red, semitransparent serum. Denis extracted the organic constituent of the corpuscles by adding to defibrinated blood about one-half its volume of a solution of sodium chloride containing one part in ten of water. Allowing this to stand for ten to fifteen hours, there appears a viscid mass, which is very carefully washed with water until all the coloring matter and the salt added have been removed. The whitish, translucid mass which remains is called globuline. Globuline is readily extracted from the blood of birds but is obtained with difficulty from the blood of the human subject.

*Hæmaglobine.*—This is the coloring matter of the red corpuscles. It has been called by different writers, hæmaglobuline or hæmatocrystalline; but the crystals called hæmatine and hæmatosine are derivatives of hæmaglobine and are not normal constituents of the blood. Hæmaglobine may be extracted from the red corpuscles by adding to them, when congealed, ether, drop by drop. A jelly-like mass is then formed, which is passed rapidly through a cloth, crystals soon appearing in the liquid, which may be separated by filtration (Gautier).

The crystals of hæmaglobine extracted from human blood are in the form either of four-sided prisms, elongated rhomboids or rectangular tablets, of a purplish-red color. They are composed of carbon, hydrogen, oxygen, nitrogen, sulphur and a small quantity of iron. They are soluble in water and in very dilute alkaline solutions, and the hæmaglobine is precipitated from these solutions by potassium ferrocyanide, mercuric nitrate, chlorine or acetic acid. The proportion of this coloring matter to the entire mass of blood is about one hundred and twenty-seven parts per thousand. It constitutes $\frac{13}{15}$ to $\frac{9}{10}$ of the dried corpuscles. A solution of hæmaglobine in one thousand parts, examined with the spectroscope, gives two dark bands between the letters D and E in Frauenhofer's scale.

Treated with oxygen or prepared in fluids in contact with the air, there occurs a union of oxygen with the coloring matter, forming what has been called oxyhæmaglobine. There can be no doubt that the oxygen enters into an intimate, though rather unstable combination with hæmaglobine, and this is an important point to be considered in connection with the absorption of oxygen by the blood in respiration. A solution of oxyhæmaglobine presents a different spectrum from that produced by a solution of pure hæmaglobine.

### Composition of the Blood-Plasma.

Assuming that the blood furnishes matters for the nourishment of all the tissues and organs, there should be found entering into its composition all the constituents of the body which undergo no change in nutrition, like the inorganic salts, and organic matters capable of being converted into the organic constituents of every tissue. Farthermore, as the products of waste are all taken up by the blood before their final elimination, these also should enter into its composition.

Most of the constituents of the blood are found both in the corpuscles and plasma. It is difficult to determine all of the different constituents of these two parts of the blood. It has been shown, however, that the phosphorized fats are more abundant in the globules, while the fatty acids are more abundant in the plasma. The salts of potassium exist almost entirely in the corpuscles, and the sodium salts are four times more abundant in the plasma than in the corpuscles (Schmidt). In addition to the nutritive matters, the blood contains urea, cholesterine, sodium urate, creatine, creatinine, and other substances, the characters of which are not yet fully determined, belonging to the class of excrementitious matters. Their consideration comes more appropriately under the head of excretion.

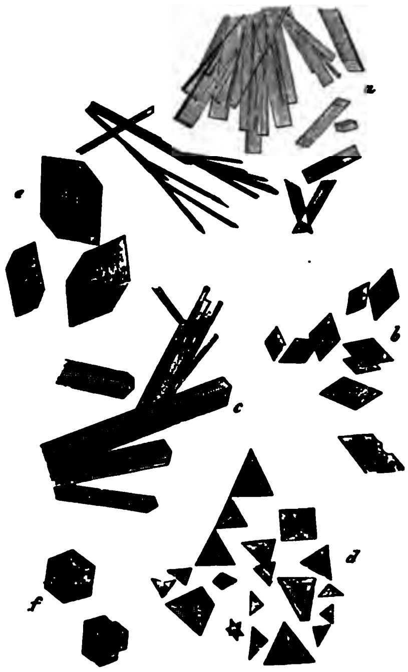

FIG. 9.—*Crystallized hæmaglobine* (Gautier). *a*, *b*, crystals from the venous blood of man; *c*, blood of the cat; *d*, blood of the Guinea pig; *e*, blood of the marmot; *f*, blood of the squirrel. (Gautier.)

The following table gives approximately the quantities of the different constituents of the blood-plasma. These may be divided into the following classes: 1. Inorganic constituents; 2. Organic saline constituents; 3. Organic non-nitrogenized constituents; 4. Excrementitious constituents; 5. Organic nitrogenized constituents. This table will be taken as a guide for the study of the individual constituents of the blood-plasma. As regards gases, in addition to carbon dioxide, which is classed with the excrementitious constituents, the blood contains oxygen, nitrogen and hydrogen. The nitrogen and hydrogen are not important, and the relations of oxygen will be fully considered in connection with the physiology of respiration. Most of the coloring matter of the blood exists in the red corpuscles, which contain a peculiar substance that has already been considered in connection with the chemical constitution of these bodies.

In studying the composition of the blood, as well as the composition of food, the tissues, secreted fluids etc., it is convenient to divide its constituents into classes, and this has been done in the simplest manner possible.

It is evident, the blood receiving all the products of disassimilation as well as the nutritive matters resulting from digestion, that there should be a division of its constituents into nutritive and excrementitious. The excrementitious matters are the products of disassimilation of the organism, which are taken up by the blood or conveyed to the blood-vessels by the lymphatics, exist in the blood in small quantity, and are constantly being separated from the blood by the different excreting organs. Their constant removal from the blood is the explanation of the minute proportion in which they exist in this fluid.

## CONSTITUENTS OF THE BLOOD-PLASMA.

**Specific gravity, 1028.**

| | | |
|---|---|---|
| Inorganic. | Water, 779 parts per 1,000 in the male; 791 parts per 1,000 in the female. | |
| | Sodium chloride, 3 to 4 parts per 1,000. | |
| | Potassium chloride, 0·359 parts per 1,000. | |
| | Ammonium chloride, proportion not determined. | |
| | Potassium sulphate, 0·288 parts per 1,000. | |
| | Sodium sulphate, proportion not determined. | |
| | Potassium carbonate, proportion not determined. | |
| | Sodium carbonate (with sodium bicarbonate), 1·200 parts per 1,000. | |
| | Magnesium carbonate, proportion not determined. | |
| | Calcium phosphate of the bones, and neutral phosphate, | 1·500 parts per 1,000. |
| | Magnesium phosphate, | |
| | Potassium phosphate, | |
| | Ferric phosphate (probable), | |
| | Basic phosphates and neutral sodium phosphate, | |
| | Silica, copper, lead, and magnesia, traces occasionally. | |
| Organic saline. | Sodium lactate, proportion not determined. | |
| | Calcium lactate (probable), proportion not determined. | |
| | Sodium oleate, | 1·475 parts per 1,000. |
| | " palmitate, | |
| | " stearate, | |
| | " valerate, | |
| | " butyrate, | |
| Organic non-nitrogenized. | Oleine, | |
| | Palmitine, | |
| | Stearine, | |
| | Lecethine, containing nitrogen and called phosphorized fatty matter, 0·400 parts per 1,000. | |
| | Glucose, 0·002 parts per 1,000. | |
| | Glycogen, proportion not determined. | |
| | Inosite, proportion not determined. | |
| Excrementitious. | Carbon dioxide in solution. | |
| | Urea, 0·177 parts per 1,000, in arterial blood; 0·088, in the blood of the renal vein. | |
| | Sodium urate, proportion not determined. | |
| | Potassium urate (probable), proportion not determined. | |
| | Calcium urate, " " " " | |
| | Magnesium urate, " " " " | |
| | Ammonium urate, " " " " | |
| | Sodium sudorates, etc., " " " | |
| | Inosates, " " " | |
| | Oxalates, " " " | |
| | Creatinine, " " " | |
| | Leucine, " " " | |
| | Hypoxanthine, " " " | |
| | Cholesterine, 0·455 to 0·751 parts per 1,000, in the entire blood. | |
| Organic nitrogenized. | Plasmine, 25 parts (dried) per 1,000. | Fibrin, [illegible] parts per 1,000. Metalbumen, 22 parts per 1,000. |
| | Serine, 53 parts (dried) per 1,000. | |
| | Peptones, 4 parts (dried) and 28 parts (moist) per 1,000. | |
| | Coloring matters of the plasma, proportion and characters not determined. | |

Excluding for the present, all consideration of the products of disassimilation, there remain the various constituents of the blood that are more or less directly concerned in nutrition.

Physiological chemists recognize certain chemical constituents of the organism, which may be elementary substances, but which are more frequently compounds. Sodium chloride is spoken of as a constituent of the blood, because, as sodium chloride, it gives to the blood certain properties. The chemical elements, chlorine and sodium, are not regarded as constituents of the blood, because they do not exist uncombined in the blood. Still, a chemical constituent may be a chemical element, as in the case of oxygen, which, as oxygen, has certain important uses in the economy; although even oxygen probably is loosely combined in the body with other matters.

A chemical constituent of the blood or of any of the animal tissues or fluids may be defined as a substance extracted from the body, which can not be subdivided without chemical decomposition and loss of certain characteristic properties. This definition will apply to all classes of chemical constituents of the body, organic as well as inorganic. The chemical elements of which the constituents are composed are properly the ingredients of the body.

The constituents of the blood, and, indeed, of the entire organism, may be classified as follows:

1. *Inorganic Constituents.*—This class is of inorganic origin, definite chemical composition and crystallizable. The substances included in this class are all introduced from without and are all discharged from the body in the same form in which they entered. They never exist alone, but are always combined with the organic constituents, and form a part of the organized fluids or solids. This union is so intimate that they are taken up with the organic matters, as the latter are worn out and become effete, and are discharged from the body, although themselves unchanged. To supply the place of the constituents thus thrown off, a fresh quantity is deposited in the process of nutrition. They give to the various organs important properties; and although identical with substances in the inorganic world, in the interior of the body they behave as organic substances. They require no special preparation for absorption, but are soluble and taken in unchanged. They are received into the body in about the same proportion at all periods of life, but their discharge is notably diminished in old age, giving rise to calcareous incrustations and deposits and a considerable increase in the calcareous matter entering into the composition of the tissues. Water, sodium chloride, the carbonates, sulphates, phosphates and other inorganic salts may be cited as examples of this class of constituents.

The uses of water in the blood are sufficiently evident. It acts as a solvent for the inorganic salts, the organic salts and the excrementitious matters. In conjunction with the nitrogenized matters, it constitutes a medium in which the corpuscles are suspended without solution.

The various salts enumerated in the table exist in solution in water and are more or less intimately combined with the coagulable organic matters. Of these, the sodium chloride is the most abundant. It undoubtedly has an important use in giving density to the plasma and in regulating the processes of endosmosis and exosmosis. In connection with the organic salts and crystallizable excrementitious matters, it may be stated, in general terms, that the blood contains 14 to 16 parts per 1,000 of matters in actual solution, of which 6 to 8 parts consist of inorganic salts. The presence of these substances in solution, with the organic coagulable matters, prevents the solution of the corpuscular elements of the blood. The presence of the chlorides and the alkaline sulphates assists in dissolving the sulphates, carbonates and the calcareous phosphates. The carbonates and phosphates are in part decomposed in the system and furnish bases for certain of the organic salts, such as the lactates, urates etc.

2. *Organic Saline Constituents.*—These substances are in greatest part formed in the organism and they exist in the blood in very small quantity. The lactates are probably produced by decomposition of a portion of the bicarbonates and the union of the bases with lactic acid, the lactic acid resulting, possibly, from a change of a portion of the saccharine matter in the blood. The physiological relations of these substances are little understood. The salts formed by the union of fatty acids with bases are probably produced by decomposition of fatty matters, a great part of which is derived from the food.

3. *Organic Non-nitrogenized Constituents.*—These usually exist in the blood in small quantity and are derived mainly from the food. Lecethine, although it contains nitrogen, is included in this class because it presents many of the properties of the fats. It exists in the blood, bile, nervous substance and the yelk of egg. Its chemical properties and physiological relations are not well understood. The saccharine matters and glycogen are derived in part from the food and in part from the liver, where glycogen is formed. They are of organic origin, definite chemical composition and crystallizable. The fats and sugars are distinguished from other organic substances by the fact that they are composed of carbon, hydrogen and oxygen. In the sugars, the hydrogen and oxygen exist in the proportion to form water, which fact has given them the name of carbohydrates. The constituents of this class play an important part in development and nutrition. One of them, sugar, appears very early in fœtal life, formed first in the placenta and afterward in the liver, its formation by the latter organ continuing during life. Fat is a necessary constituent of food and is also formed in the interior of the body. The exact influence which these substances have on development and nutrition is not known; but experiments and observation have shown that this influence is important. They will be considered more fully in connection with the physiology of nutrition.

4. *Excrementitious Constituents.*—A full consideration of these substances, which are all formed by the process of disassimilation of the tissues and are taken up by the blood to be eliminated by the proper organs, be-

longs to the physiology of excretion. The relations of carbon dioxide to the system will be fully considered in connection with the physiology of respiration.

5. *Organic Nitrogenized Constituents.*—This class of constituents is of organic origin, indefinite chemical composition and non-crystallizable. The constituents included in this class are apparently the only matters that are endowed with so-called vital properties, taking materials for their regeneration from the nutritive fluids and appropriating them to form part of their own substance. Considered from this point of view, they are different from any substances met with out of the living body. They are all, in the body, in a state of continual change, wearing out and becoming effete, when they are transformed into excrementitious substances. The process of repair in this instance is not the same as in inorganic substances, which enter and are discharged from the body without undergoing any change. The analogous substances which exist in food undergo elaborate preparation by digestion, before they can even be absorbed by the blood-vessels; and still another change takes place when they are appropriated by the various tissues. They exist in all the solids, semi-solids and fluids of the body, never alone, but always combined with inorganic substances. As a peculiarity of chemical constitution, they all contain nitrogen, which has given them the name of nitrogenized or azotized matters.

Of the different classes of constituents of the blood, it is at once apparent that the organic nitrogenized matters are more complex in their constitution, properties and uses than the other classes. These substances, as they exist in the blood, possess certain peculiar and characteristic properties.

*Plasmine, Fibrin, Metalbumen, Serine.*—The name plasmine was given by Denis to a substance which he extracted from the blood by the following process: The blood drawn directly from an artery or vein is received into a vessel containing one-seventh part of its volume of a concentrated solution of sodium sulphate, which prevents coagulation; in a short time the corpuscles gravitate to the bottom of the vessel, and the plasma may be separated by decantation; to the plasma is added an excess of pulverized sodium chloride, when a soft, pulpy substance is precipitated, which is plasmine. This substance, after desiccation, bears a proportion of about twenty-five parts per thousand of blood. It is soluble in ten to twenty parts of water, when a portion of it coagulates and may be removed by stirring with twigs or a bundle of broom-corn, in the way in which fibrin is separated from the blood. The fibrin thus separated is called by Denis concrete fibrin, and the substance which remains in solution, dissolved fibrin. By most writers of the present day, the dissolved fibrin of Denis is called metalbumen.

According to Denis, plasmine is a proper constituent of the blood, and after extraction by the process just described, it is decomposed into concrete fibrin and dissolved fibrin, or metalbumen. Having removed the concrete fibrin from the solution of plasmine, the metalbumen is coagulated by the addition of magnesium sulphate, which does not coagulate ordinary albumen. The proportion of dried metalbumen in the blood is about twenty-two parts per thousand. The proportion of dried fibrin is about three parts per thousand.

After the extraction of plasmine from the blood, another coagulable substance remains, which is called serine. This is coagulated by heat, the strong mineral acids or absolute alcohol, but is not coagulated by ether, which coagulates egg-albumen. Serine bears a close resemblance to ordinary albumen but is much more osmotic. Its proportion, desiccated, in the blood is about fifty-three parts per thousand.

*Peptones etc.*—A certain quantity of nitrogenized matter, distinct from the constituents just described, has been extracted from the blood, which is analogous to peptone. This is separated by coagulating the serum of the blood with hot acetic acid and filtering, when the peptones pass through in the filtrate. These substances are probably derived from the food. Their proportion in the plasma is about four parts, dried, per thousand, or twenty-eight parts before desiccation.

A small quantity of coloring matter exists in the plasma. If the corpuscles be separated as completely as possible, the clear liquid still has a reddish-amber color. This coloring matter has never been isolated and studied. It is analogous to the coloring matter of the red corpuscles, the bile and the urine.

In addition to the organic nitrogenized constituents which have just been described, some physiological chemists recognize a substance called paraglobuline, or fibrinoplastic matter, and fibrinogenic matter. These are supposed to be factors of fibrin, which come together in the coagulation of the blood. They will be considered in connection with the theories of coagulation. The so-called sodium and potassium albuminates have not been positively established as normal constituents of the blood.

## Coagulation of the Blood.

The blood retains its fluidity while it remains in the vessels and circulation is not interfered with, and is then composed of a clear plasma holding corpuscles in suspension. Soon after the circulation is interrupted or after blood is drawn from the vessels, it coagulates or "sets" into a jelly-like mass. In a few hours, contraction will have taken place, and a clear, straw-colored fluid expressed, the blood thus separating into a solid portion, the crassamentum, or clot, and a liquid which is called serum. The serum contains all the constituents of the blood except the corpuscles and fibrin-factors, which together form the clot. Coagulation takes place in the blood of all animals, beginning a variable time after its removal from the vessels. In the human subject, when the blood is received into a moderately deep, smooth vessel, the phenomena of coagulation present themselves in the following order:

First, a gelatinous pellicle forms on the surface, which occurs in one minute and forty-five seconds to six minutes; in two to seven minutes, a gelatinous layer has formed on the sides of the vessel; and the whole mass becomes of a jelly-like consistence, in seven to sixteen minutes. Contraction then begins, and little drops of clear serum make their appearance on the surface of the clot. This fluid increases in quantity, and in ten or twelve hours separation is complete (Nasse). The clot, which is heavier, sinks to the bottom of the vessel, unless it contain bubbles of gas or the surface be very concave. In most of the warm-blooded animals, the blood coagulates more rapidly than in man. Coagulation is particularly rapid in blood taken from birds, and sometimes it takes place almost instantaneously. Coagulation is more rapid in arterial than in venous blood. In the former, the proportion of fibrin formed is notably greater and the characters of the fibrin are somewhat different. A solution of sodium chloride dissolves the fibrin of venous blood, but does not dissolve the fibrin of an arterial clot.

The relative proportions of the serum and clot are very variable, unless that portion of the serum which is retained between the meshes of the coagulated mass be included in the estimate. As the clot is composed of corpuscles and fibrin, and as these in their moist state represent, in general terms, about one-half of the blood, it may be stated that after coagulation, the actual proportions of the clot and serum are about equal. Simply taking the serum which separates spontaneously, there is a large quantity when the clot is densely contracted, and a very small quantity, when it is loose and soft. Usually the clot retains about one-fifth of the serum.

On removing the clot, after the separation of the serum is complete, it presents a gelatinous consistence, and is more or less firm according to the degree of contraction which has taken place. As a general rule, when coagulation has been rapid, the clot is soft and but slightly contracted. When, on the other hand, coagulation has been slow, the clot contracts for a long time and is much denser. When coagulation is slow, the clot frequently presents what is known as the cupped appearance, having a concave surface, a phenomenon which depends merely on the degree of its contraction. It also presents a marked difference in color at its upper portion. The blood having remained fluid for some time, the red corpuscles settle, by reason of their greater weight, leaving a colorless layer on the top. This is the buffy-coat spoken of by some authors. Examined microscopically, the buffy-coat presents fibrils of coagulated fibrin with some of the white corpuscles of the blood. On removing a clot of venous blood from the serum, the upper surface is florid from contact with the air, while the rest of it is dark; and on making a section, if coagulation have not been too rapid, the gravitation of the red corpuscles is apparent. If the clot be cut into small pieces, it will undergo farther contraction and express a part of the contained serum. If the clot be washed under a stream of water, at the same time kneading it with the fingers, nearly all the red corpuscles may be removed, leaving the meshes of fibrin.

After coagulation, if the serum be carefully removed, it is found to be a fluid of a color varying between a light amber and a clear red. This color depends upon a peculiar coloring matter which has never been isolated. The specific gravity of the serum is about 1028, somewhat less than that of the entire mass of blood. It presents all the constituents of the plasma, or liquor sanguinis, with the exception of the fibrin-factors. It can hardly be called a physiological fluid, as it is formed only after coagulation of the blood.

Coagulation of the blood is due to the formation of fibrin. Coagulation of this substance first causes the whole mass of blood to assume a gelatinous consistence; and by reason of its contractile properties, it soon expresses the serum, while the red corpuscles are retained. One of the causes which operate to retain the corpuscles in the clot is the adhesive matter which covers their surface after they escape from the vessels.

*Conditions which modify Coagulation.*—Blood flowing slowly from a small orifice is more rapidly coagulated than when it is discharged in a full stream from a large orifice. If it be received into a shallow vessel, it coagulates much more rapidly than when received into a deep vessel. If the vessel be rough, coagulation is more rapid than if it be smooth and polished. If the blood, as it flows, be received on a cloth or a bundle of twigs, it coagulates almost instantaneously. In short, it appears that all conditions which favor exposure of the blood to the air hasten its coagulation. The blood will coagulate more rapidly in a vacuum than in the air.

Coagulation of the blood is prevented by rapid freezing, but it takes place afterward when the fluid is carefully thawed. Between 32° and 140° Fahr. (zero and 60° C.), elevation of temperature increases the rapidity of coagulation. Agitation of the blood in closed vessels retards, and in open vessels, hastens coagulation.

Various chemical substances retard or prevent coagulation. Among them may be mentioned the following: solutions of potassium or of sodium hydrate; sodium carbonate; ammonium carbonate; potassium carbonate; ammonia; sodium sulphate. In the menstrual flow, the blood is kept fluid by mixture with the abundant secretions of the vaginal mucous membrane.

*Coagulation of the Blood in the Organism.*—The blood coagulates in the vessels after death, though less rapidly than when removed from the body. As a general proposition, it may be stated that this takes place between twelve and twenty-four hours after circulation has ceased. Under these conditions, the blood is found chiefly in the venous system, as the arteries are usually emptied by post-mortem contraction of their muscular coat; but in the veins, coagulation is slow and imperfect. Coagula are found, however, in the left side of the heart and in the aorta, but they are much smaller than those in the right side of the heart and in the large veins. These coagula present the general characters already described. They are frequently covered by a soft, whitish film and are dark in their interior.

It was supposed by John Hunter that coagulation of the blood did not take place in animals killed by lightning, or by prolonged muscular exertion, as when hunted to death; but it appears from the observations of others that this view is not correct. J. Davy reported a case of death by lightning, in which a loose coagulum was found in the heart twenty-four hours after. In this case decomposition was very far advanced, and it is probable that the coagulum had become less firm from that cause. His observations also show that coagulation occurs after poisoning by hydrocyanic acid and in animals hunted to death.

Coagulation in different parts of the vascular system is by no means unusual during life. In the heart, coagula which bear evidence of having existed for some time before death are sometimes found. These were called polypi by some of the older writers and are often formed of fibrin almost free from red corpuscles. They generally occur when death is very gradual and when the circulation continues for some time with greatly diminished activity. It is probable that a small coagulum is first formed, from which the corpuscles are washed away by the current of blood; and that this becomes larger by farther depositions, until large, vermicular masses of fibrin are found attached, in some instances, to the chordæ tendineæ. Bodies projecting into the caliber of a blood-vessel soon become coated with a layer of fibrin. Rough concretions about the orifices of the heart frequently lead to the deposition of little masses of fibrin, which sometimes become detached and are carried to various parts of the circulatory system, as the lungs or brain, plugging up one or more of the smaller vessels. Blood generally coagulates when effused into the areolar tissue or into any of the cavities of the body; although, effused into the serous cavities, the tunica vaginalis for example, it has been known to remain fluid for days and even weeks, and coagulate when let out by an incision. Coagulation thus takes place in the vessels as the result of stasis or of very great retardation of the circulation, and in the tissues or cavities of the body, whenever it is accidentally effused. In the latter case, it is generally removed in the course of time by absorption.

The property of the blood under consideration has an important office in the arrest of hæmorrhage. The effect of an absence or great diminution of the coagulability of the circulating fluid is exemplified in instances of what is called the hæmorrhagic diathesis, or hæmophilia; a condition in which slight wounds are likely to be followed by alarming, and it may be fatal hæmorrhage. This condition of the blood is not characterized by any peculiar symptoms except the obstinate flow of blood from slight wounds; and it may continue for years.

Conditions which accelerate coagulation have a tendency to arrest hæmorrhage. It is well known that exposure of a bleeding surface to the air has this effect. The way in which the vessel is divided has an important influence. A clean cut will bleed more freely than a ragged laceration. In division of large vessels, this difference is sometimes very marked. Cases are on record in which the arm has been torn off at the shoulder-joint, and yet the hæmorrhage was, for a time, spontaneously arrested; while it is well known that division of an artery of comparatively small size, if it be cut across, would be fatal if left to itself. Under these conditions, the internal coat is torn in shreds which retract, their curled ends projecting into the caliber of the vessel and having the same effect on the coagulation of blood as a bundle of twigs. In laceration of such a large vessel as the axillary artery, the arrest can not be permanent, for as soon as the system recovers from the shock, the contractions of the heart force out the coagulated blood which has closed the opening.

From the foregoing considerations, it is evident that coagulation of the blood has for its chief office the arrest of hæmorrhage. Coagulation never takes place in the organism unless the blood be in an abnormal condition with respect to circulation. Here its operations are mainly conservative; but as almost all conservative processes are sometimes perverted, clots in the body may be productive of injury, as in the instances of cerebral apoplexy, clots in the heart occurring before death, the detachment of emboli etc.

*Cause of the Coagulation of the Blood.*—Alex. Schmidt, in 1861, proposed a theory of coagulation, which involves the coming together of certain matters called fibrin-factors. This theory, which had been indicated by Buchanan, in 1845, has been adopted and more or less modified by Kühne, Virchow and others. If blood-plasma, rendered neutral with acetic acid, be diluted with ten times its volume of water at 32° Fahr. (zero C.), and then be treated with a current of carbon dioxide, a flocculent precipitate is formed, which has been called paraglobuline, or fibrinoplastic matter. This substance may be dissolved in water containing air or oxygen in solution. After this precipitate has been separated, if the clear liquid be diluted with about twice its volume of ice-cold water and be treated for two or three hours with a current of carbon dioxide, a viscid scum is produced, which has been called fibrinogen. More recently, a third principle, a ferment, has been described by Schmidt, which he considers necessary to the formation of fibrin. This ferment is produced in some way by the leucocytes of the blood, probably by partial decomposition of these bodies.

In view of the results of recent investigations with regard to the cause of the coagulation of the blood, which, unfortunately, are not as positive and definite as could be desired, some physiologists have adopted the following as a provisional theory of the mechanism of this process:

There exists, probably in small quantity in the circulating blood and in considerable quantity in blood drawn from the vessels or arrested in its circulation, a peculiar ferment which is produced in some way by changes in the leucocytes. This ferment may be concerned in the decomposition of plasmine. It is certainly thrown down with plasmine when plasmine is precipitated by the action of reagents. The action of this ferment either induces or hastens the separation of plasmine into the so-called fibrin-factors, paraglobuline and fibrinogen. Of these two substances, fibrinogen is the more important in the formation of fibrin, a small quantity of fibrin, only about three parts per thousand of blood, being formed. A large quantity of paraglobuline is not used in the formation of fibrin and remains in the serum. It is possible, indeed, that no part of the paraglobuline is concerned in coagulation. If the latter be true, paraglobuline may be regarded as identical with metalbumen, a view which was advanced by Robin many years ago and is now adopted by some physiologists.

Adopting these views, the mechanism of coagulation may be succinctly described as follows:

1. As a condition preliminary to coagulation, there is either an increase in the formation of fibrin-ferment or an appearance of ferment in the blood, due to changes in certain of the leucocytes. The red corpuscles are probably not directly concerned in coagulation, and there is nothing definite known of the action of the blood-plaques in this process.

2. The fibrin-ferment unites with fibrinogen and forms fibrin, which is the coagulating substance. Paraglobuline (or metalbumen) is little if at all concerned in this process.

3. The processes described as incident to the coagulation of blood take place also in the coagulation of lymph and chyle.

In accordance with the views stated in connection with the composition of blood-plasma, paraglobuline, or metalbumen, fibrinogen and, finally, fibrin are products of decomposition, are abnormal formations, and are not normal constituents of the blood.

It is possible that the statement just given of the mechanism of the coagulation of the blood may be modified in the future in accordance with the most recent views of Schmidt, who claims that all the so-called fibrin-factors result from decomposition of the leucocytes, a great number of which, it is said, are dissolved soon after blood is drawn from the vessels. There are, indeed, many experimental and pathological facts in support of this view; but it can not be adopted without reserve, until the experiments of Schmidt shall have been supplemented by more extended observations. Schmidt maintains that in certain classes of animals, dissolved red corpuscles are also concerned in the production of fibrin-factors.

Leech-drawn blood remains fluid in the body of the animal. Richardson has observed, also, that the blood flowing from a leech-bite presents the same persistent fluidity, which explains the well-known fact that the insignificant wound gives rise to considerable hæmorrhage.

The existence of projections into the caliber of vessels, or the passage of a fine thread through an artery or vein, will determine the formation of a small coagulum upon the foreign substance, while the circulation is neither interrupted nor retarded. In the present state of knowledge, explanation of these facts is difficult if not impossible. The process, under these conditions, can not be subjected to direct experiment as in the case of blood coagulating out of the body.

FIG. 10.—*Coagulated fibrin* (Robin).
Fibrinous clot, without red corpuscles, and containing leucocytes, thrown off in the form of a whitish pseudo-membrane in a case of ulceration of the neck of the uterus with hæmorrhage.

During coagulation, fibrin assumes a filamentous form, presenting, under the microscope, the appearance of rectilinear fibrillæ. These fibrillæ gradually increase in number, and as contraction of the clot occurs, they become irregularly crossed. They are always straight, however, and never assume the wavy appearance characteristic of true fibrous tissue.

The blood of the renal and hepatic veins, capillary blood and the blood which passes from the capillary system into the veins after death generally does not coagulate or coagulates very imperfectly; in other words, these varieties of blood do not readily form fibrin. The reason of this peculiarity is not known; but the fact affords a partial explanation of the normal fluidity of the blood; for this fluid, passing over the entire course of the circulation in about thirty seconds, seems to be constantly losing its coagulability in its passage through the liver, kidneys and the general capillary system, as fast as its coagulability is increased in the other parts. Taking into consideration the rapidity of the circulation, it is evident that coagulation can not take place while the normal circulation is maintained and while the blood is undergoing the constant changes incident to general nutrition.

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# CHAPTER II.

## *CIRCULATION OF THE BLOOD—ACTION OF THE HEART.*

Discovery of the circulation—Physiological anatomy of the heart—Valves of the heart—Movements of the heart—Impulse of the heart—Succession of the movements of the heart—Force of the heart—Action of the valves—Sounds of the heart—Causes of the sounds of the heart—Frequency of the heart's action—Influence of age and sex—Influence of digestion—Influence of posture and muscular exertion—Influence of exercise etc.—Influence of temperature—Influence of respiration on the action of the heart—Cause of the rhythmical contractions of the heart—Accelerator nerves—Direct inhibition of the heart—Reflex inhibition of the heart—Summary of certain causes of arrest of the action of the heart.

Harvey "set forth for the first time his discovery of the circulation," in his public lectures in 1616, and in 1628 published the "*Exercitatio Anatomica de Motu Cordis et Sanguinis in Animalibus.*" This discovery, from the isolated facts bearing upon it which were observed by anatomists to its culmination in the experiments of Harvey, so fully illustrates the gradual development of most physiological truths, that it does not seem out of place to begin the study of the circulation with a brief sketch of its history.

The facts bearing upon the circulation developed before the time of Harvey were chiefly anatomical. The writings of Hippocrates are very indefinite upon all points connected with the circulatory system; and no clear and positive statements are to be found in ancient works before the time of Aristotle. The work of Aristotle most frequently quoted by physiologists is his "History of Animals;" and in this occurs a passage which seems to indicate that he thought that air passed from the lungs to the heart; but in his work, *De Partibus Animalium*, it is stated that there are two great blood-vessels, the vena cava and aorta, arising from the heart, and that the aorta and its branches carry blood. Galen, however, demonstrated experimentally the presence of blood in the arteries, by including a portion of one of these vessels between two ligatures, in a living animal; but his ideas of the communication between the arteries and veins were erroneous, for he believed in the existence of small orifices in the septum between the ventricles of the heart, a mistake that was corrected by Vesalius, at about the middle of the sixteenth century.

In 1553, Michael Servetus, who is generally regarded as the discoverer of the passage of the blood through the lungs, or the pulmonary circulation, described in a work on theology the course of the blood through the lungs, from the right to the left side of the heart. This description, complete as it is, was merely incidental to the development of a theory with regard to the formation of the soul and the development of what were called animal and vital spirits (*spiritus*).

A few years later, Colombo, professor of anatomy at Padua, and Cesalpinus, of Pisa, described the passage of the blood through the lungs, though probably without any knowledge of what had been written by Servetus. To Cesalpinus is attributed the first use of the expression circulation of the blood; and he also remarked that after ligature or compression of veins, the swelling is always below the point of obstruction.

The history of the discovery of the valves in the veins is quite obscure, although priority of observation is almost universally conceded to Fabricius. As regards this point, only the dates of published memoirs are to be considered, notwithstanding the assertion of Fabricius that he had seen the valves in 1574. In 1545, Étienne described, in branches of the portal vein, "valves, which he called apophyses, and which he compared to the valves of the heart." In 1551, Amatus Lusitanus published a letter from Cannanus, in which it is stated that he had found valves in certain of the veins. In 1563, Eustachius published an account of the valves of the coronary vein. In 1586, a clear account, by Piccolhominus, of the valves of the veins was published. Fabricius gave the most accurate descriptions and delineations of the valves, and his first publication is said to have appeared in 1603. He demonstrated the valves to Harvey, at Padua; and it is probable that this was the origin of the first speculations by Harvey on the mechanism of the circulation.

In the work of Harvey are described, first the movements of the heart, which he exposed and studied in living animals. He described minutely all the phenomena which accompany its action; its diastole, when it is filled with blood, and its systole, when the fibres of which the ventricles are composed contract simultaneously, and "by an admirable adjustment all the internal surfaces are drawn together, as if with cords, and so is the charge of blood expelled with force." From the description of the action of the ventricles, he passed to the auricles, and showed how these, by their contraction, filled the ventricles with blood. By experiments upon serpents and fishes, he proved that the blood fills the heart from the veins and is sent out into the arteries. Exposing the heart and great vessels in these animals, he applied a ligature to the veins, which had the effect of cutting off the supply from the heart so that it became pale and flaccid; and by removing the ligature the blood could be seen flowing into the organ. When, on the contrary, a ligature was applied to the artery, the heart became unusually distended, which continued so long as the obstruction remained. When the ligature was removed, the heart soon returned to its normal condition. Harvey completed his description of the circulation, by experiments showing the course of the blood in the arteries and veins and the uses of the valves of the veins.

By these simple experiments, the chain of evidence establishing the fact of the circulation of the blood was completed. Truly it is said that here began an epoch in the study of physiology; for then scientific observers began to emancipate themselves from the ideas of the ancients, which had controlled opinions for two centuries, and to study Nature for themselves by means of experiments.

Although Harvey described so perfectly the course of the blood and left no doubt as to the communication between the arteries and veins, it was left to others to actually see the blood in movement and follow it from one system of vessels to the other. In 1661, Malpighi saw the blood circulating in the vessels of the lung of a living frog, examining it with magnifying glasses; and a little later, Leeuwenhoek saw the circulation in the wing of a bat. These observations completed the discovery of the circulation.

In man and in the warm-blooded animals, the organism requires blood that has been oxygenated in the lungs, and to meet this demand fully, the circulatory system is divided into pulmonic and systemic. The heart is double, having a right side and a left side, which are entirely distinct from each other. The right heart receives the blood as it is brought from the general system by the veins and sends it to the lungs; the left heart receives the blood from the lungs and sends it to the general system. It must be borne in mind, however, that although the two sides of the heart are distinct from each other, their action is simultaneous; and in studying the motions of the heart, it will be found that the blood is sent simultaneously from the right side to the lungs and from the left side to the system. It will not be necessary, therefore, to separate the two circulations in the study of their mechanism; for the simultaneous action of both sides of the heart renders it possible to study its action as a single organ, and the constitution and operations of the two kinds of vessels do not present any material differences.

For convenience of study, the circulatory system may be divided into heart and vessels, the latter being of three kinds: the arteries, which carry blood from the heart to the general system; the capillaries, which distribute the blood more or less abundantly in different parts of the general system; and the veins, which return the blood from the general system to the heart.

### Physiological Anatomy of the Heart.

The heart of the human subject is a pear-shaped, muscular organ, situated in the thoracic cavity, with its base in the median line and its apex at the fifth intercostal space, three inches (7·6 centimetres) to the left of the median line, or one inch (2·5 centimetres) within the line of the left nipple.

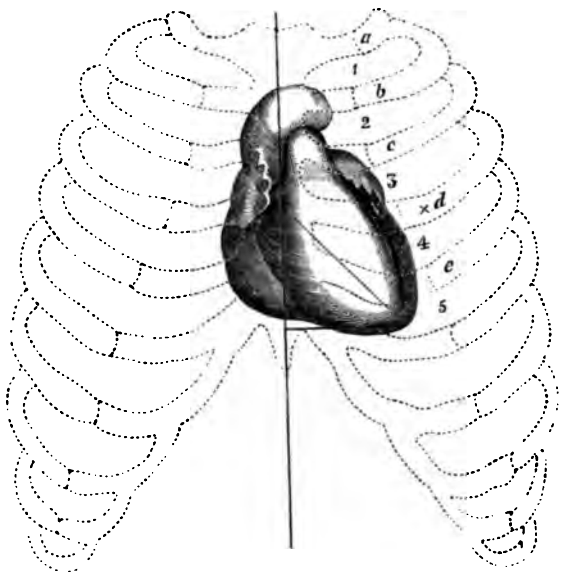


FIG. 11.—*Heart in situ* (Dalton, in Flint, "on the heart"). *a*, *b*, *c* etc., ribs; 1, 2, 3 etc., intercostal spaces; vertical line, median line; triangle, superficial cardiac region; × on the fourth rib, nipple.

Its weight is eight to ten ounces (227 to 283 grammes) in the female, and ten to twelve ounces (283 to 340 grammes) in the male. It has four distinct cavities; a right and a left auricle, and a right and a left ventricle. Of these, the ventricles are the more capacious. The heart is held in place by the attachment of the great vessels to the posterior wall of the thorax; while the apex is free and capable of a certain degree of motion. The whole organ is enveloped in a fibrous sac called the pericardium. This sac is lined by a serous membrane, which is attached to the great vessels at the base and reflected over its surface. The membrane is lubricated by about a drachm (3·7 c. c.) of fluid, so that the movements of the heart are normally accomplished without any friction. The serous pericardium does not present any differences from serous membranes in other situations. The cavities of the heart are lined by a smooth membrane called the endocardium, which is continuous with the lining membrane of the blood-vessels.

The right auricle receives the blood from the venæ cavæ and empties it into the right ventricle. The auricle presents a principal cavity, or sinus, as it is called, with a little appendix, called, from its resemblance to the ear of a dog, the auricular appendix. It has two large openings for the vena cava ascendens and the vena cava descendens respectively, with a small opening for the coronary vein which brings the blood from the substance of the heart itself. It has, also, another large opening, called the auriculo-ventricular opening, by which the blood flows into the ventricle. The walls of this cavity are quite thin as compared with the ventricles, measuring about one line (2·1 mm.). They are composed of muscular fibres arranged in two layers, one of which, the external, is common to both auricles, and the other, the internal, is proper to each. These muscular fibres, although involuntary in their action, belong to the striated variety, and are similar in structure to the fibres of the ventricles. The fibres of the auricles are much fewer than those of the ventricles. Some of them are looped, arising from a cartilaginous ring which separates the auricles and ventricles and passing over the auricles; and others are circular, surrounding the auricular appendages and the openings of the veins, extending, also, a short distance along the course of these vessels. One or two valvular folds are found at the orifice of the coronary vein, preventing a reflux of blood, but there are no valves at the orifices of the venæ cavæ.

FIG. 12.—*Course of the muscular fibres of the left auricle* (Landois).

The left auricle receives the blood which comes from the lungs by the pulmonary veins. It does not differ materially in its anatomy from the right. It is a little smaller, and its walls are thicker, measuring about a line and a half (3·15 mm.). It has four openings by which it receives the blood from the four pulmonary veins. These openings are not provided with valves. Like the right auricle, it has a large opening by which blood flows into the corresponding ventricle. The arrangement of the muscular fibres is essentially the same as in the right auricle. In adult life, the cavities of the auricles are entirely distinct from each other. Before birth, they communicate by a large opening, the foramen ovale, and the orifice of the inferior vena cava is provided with a mem-

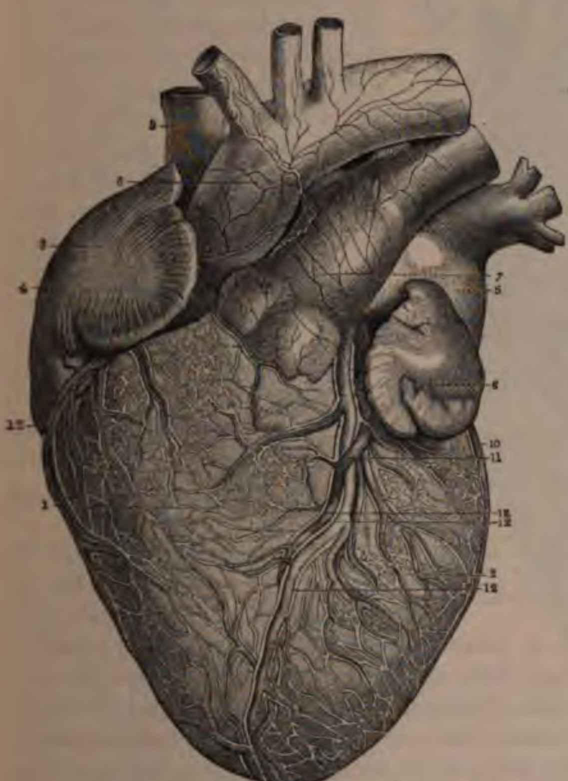

FIG. 13.—*Heart, anterior view* (Bonamy and Beau).
1, *right ventricle*; 2, *left ventricle*; 3, 4, *right auricle*; 5, 6, *left auricle*; 7, pulmonary artery; 8, aorta; 9, superior vena cava; 10, anterior coronary artery; 11, branch of the coronary vein; 12, 12, 12, lymphatic vessels.

branous fold, the Eustachian valve, which serves to direct the blood from the lower part of the body through the opening into the left auricle. After birth, the foramen ovale is closed and the Eustachian valve gradually disappears.

The ventricles, in the human subject and in warm-blooded animals, constitute the bulk of the heart. They have a capacity somewhat greater than that of the auricles and are provided with thick, muscular walls. It is by the powerful action of this portion of the heart that the blood is forced, on the one hand, to the lungs and back to the left side of the heart, and on the other, through the entire system of the greater circulation, to the right side.

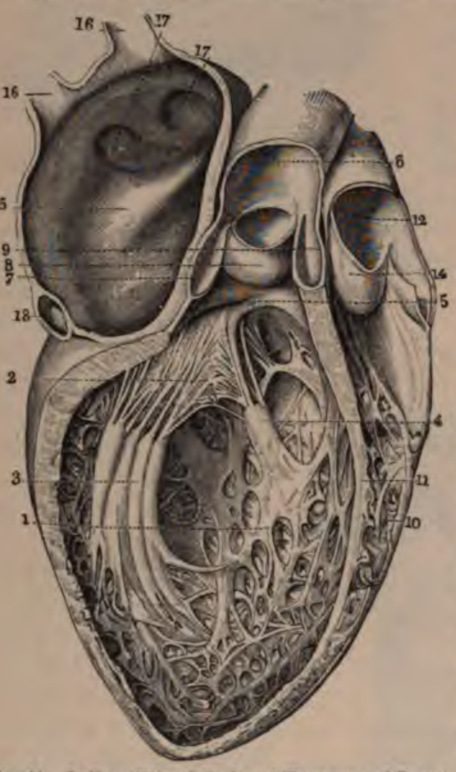


FIG. 14.—*Left cavities of the heart* (Bonamy and Beau.) 1, *left ventricular cavity*; 2, *mitral valve*; 3, 4, *columnæ carneæ*; 5, *aortic opening*; 6, *aorta*; 7, 8, 9, *aortic valves*; 10, right ventricular cavity; 11, interventricular septum; 12, pulmonary artery; 13, 14, pulmonic valves; 15, left auricular cavity; 16, 16, right pulmonary veins, with 17, 17, openings of the veins; 18, section of the coronary vein.

The capacity of the cavities on the right side of the heart is one-tenth to one-eighth greater than that of the corresponding cavities on the left side. The capacity of the ventricles exceeds that of the auricles by one-fourth to one-third. The absolute capacity of the left ventricle, when distended to its utmost (Robin and Hiffelsheim), is 4·8 to 7 ounces (143 to 212 c. c.). This is much greater than most estimates, which place the capacity of each of the various cavities, moderately distended, at about two ounces (59·1 c. c.); but the observations of Robin and Hiffelsheim, upon the human heart, were made evidently with the greatest accuracy, either before cadaveric rigidity had set in or after it had disappeared.

Notwithstanding the disparity in the extreme capacity of the various cavities, the quantity of blood which enters these cavities is necessarily equal to that which is expelled. This has been stated to be a little more than two ounces (about 60 c.c.). There are, however, no means of estimating with exactness the quantity of blood discharged with each ventricular contraction; and the question seems to be rather avoided in many works on physiology. Judging, however, from observations on the heart during its action, it never seems to contain much more than half the quantity in all its cavities that it does when fully distended by injection; but the right cavities are more dilatable than the left, and probably the ordinary quantity of blood in the left ventricle is four-fifths to five-sixths of its extreme capacity, or five to six ounces (120 to 170 c.c.).

The cavities of the ventricles are triangular or conoidal, the right being broader and shorter than the left, which latter extends to the apex. The inner surface of both cavities is marked by ridges and papillæ, which are called columnæ carneæ. Some of these are fleshy ridges projecting into the cavity; others are columns attached by each extremity and free at the central portion; and others are papillæ giving origin to the chordæ tendineæ, which are attached to the free edges of the auriculo-ventricular valves. These fleshy columns interlace in every direction and give the inner surface of the cavities a reticulated appearance. This arrangement facilitates the complete emptying of the ventricles during their contraction.

The walls of the left ventricle are uniformly much thicker than those of the right side. The average thickness of the right ventricle at the base is two and a half lines (5·25 mm.), and the thickness of the left ventricle at the corresponding part is seven lines (14·7 mm.), or a little more than half an inch (Bouillaud).

FIG. 15.—*Right cavities of the heart* (Bonamy and Beau). 1, *right ventricular cavity*; 2, *posterior curtain of the tricuspid valve*; 3, *right auricular cavity*; 4, *columnæ carneæ of the right auricle*; 5, section of the coronary vein; 6, Eustachian valve; 7, ring of Vieussens; 8, fossa ovalis; 9, superior vena cava; 10, inferior vena cava; 11, aorta; 12, 12, right pulmonary veins.

The arrangement of the muscular fibres constituting the walls of the ventricles is more regular than in the auricles, and their course affords an explanation of some of the phenomena which accompany the heart's action. The direction of the fibres can not be well made out unless the heart have been boiled for a number of hours, when part of the intermuscular tissue is dissolved out, and the fibres can be easily separated and followed. Without entering into a minute description of their direction, it is sufficient to state, in this connection, that they present two principal layers; a superficial layer common to both ventricles, and a deep layer proper to each ventricle. The superficial fibres pass obliquely from right to left from the base to the apex; here they take a spiral course, become deep, and pass into the interior of the organ, to form the columnæ carneæ. These fibres envelop both ventricles. They may be said to arise from cartilaginous rings which surround the auriculo-ventricular orifices. The external surface of the heart is marked by a little groove which indicates the division between the two ventricles. The deep fibres are circular, or transverse, and surround each ventricle separately.

The muscular tissue of the heart is of a deep-red color and resembles, in its gross characters, the tissue of ordinary voluntary muscles; but as already intimated, it presents certain peculiarities in its minute anatomy. The fibres are considerably smaller and more granular than those of ordinary muscles. They are, moreover, connected with each other by short, inosculating branches. (See Fig. 17.) The muscular fibres of the heart have no sarcolemma. These peculiarities, particularly the inosculation of the fibres, favor the contraction of the ventricular walls in every direction and the complete expulsion of the contents of the cavities with each systole.

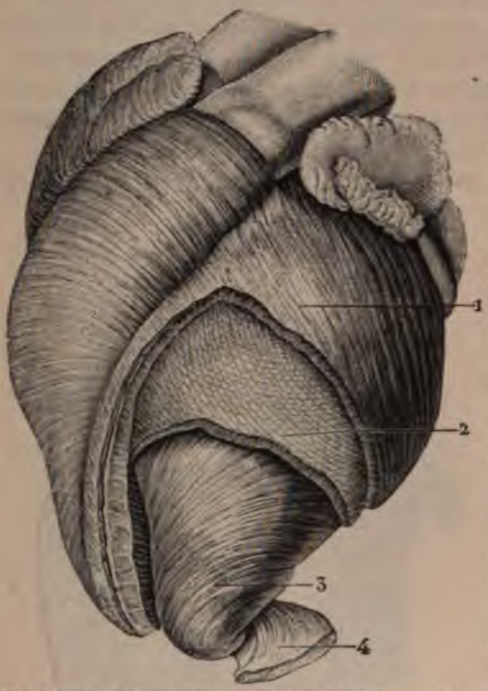


FIG. 16.—*Muscular fibres of the ventricles* (Bonamy and Beau).

1, superficial fibres common to both ventricles; 2, fibres of the left ventricle; 3, deep fibres passing upward toward the base of the heart; 4, fibres penetrating the left ventricle.

The distribution of the nerves to the heart and the arrangement of the ganglia and nerve-terminations in its substance will be described in connection with the influence of the nervous system upon the circulation.

Each ventricle has two orifices; one by which it receives the blood from the auricle, and the other by which the blood passes from the right side to the lungs and from the left side to the general system. All of these openings are provided with valves, which are so arranged as to allow the blood to pass in but one direction.

*Tricuspid Valve.*—This valve is situated at the right auriculo-ventricular opening. It has three curtains, formed of a thin but resisting membrane, which are attached around the opening. The free borders are attached to the chordæ tendineæ, some of which arise from the papillæ on the inner surface of the ventricle, and others, directly from the walls of the ventricle. When the organ is empty, these curtains are applied to the walls of the ventricle, leaving the auriculo-ventricular opening free; but when the ventricle is completely filled and the fibres contract, they are forced up, their free edges become applied to each other, and the opening is closed.

*Pulmonic Valves.*—These valves, also called the semilunar, or sigmoid valves of the right side, are situated at the orifice of the pulmonary artery. They are strong, membranous pouches, with their convexities, when closed, looking toward the ventricle. They are attached around the orifice of the pulmonary artery and are applied very nearly to the walls of the vessel when the blood passes in from the ventricle; but at other times their free edges meet in the centre, opposing the regurgitation of blood. At the centre of the free edge of each valve is a little corpuscle called the corpuscle of Arantius; and just above the margins of attachment of the valves, the artery presents three little dilatations, or sinuses, called the sinuses of Valsalva. The corpuscles of Arantius probably aid in the adaptation of the valves to each other and in the effectual closure of the orifice.

FIG. 17.—*Branched muscular fibres from the heart of a mammal* (Landois).

*Mitral Valve.*—This valve, sometimes called the bicuspid, is situated at the left auriculo-ventricular orifice. It is called mitral from its resemblance, when open, to a bishop's mitre. It is attached to the edges of the auriculo-ventricular opening, and its free borders are held in place, when closed, by the chordæ tendineæ of the left side. It presents no material difference from the tricuspid valve, with the exception that it is divided into two curtains instead of three.

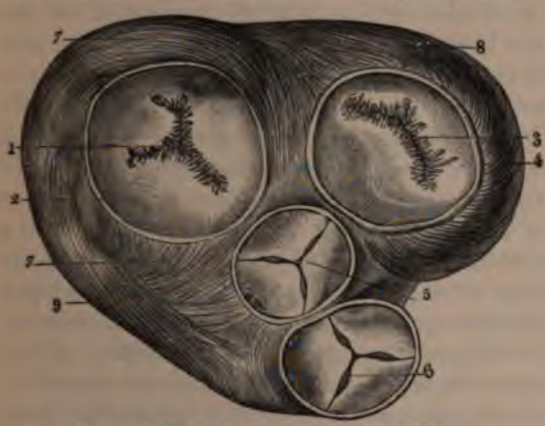


FIG. 18.—*Valves of the heart* (Bonamy and Beau).
1, right auriculo-ventricular orifice, closed by the tricuspid valve; 2, fibrinous ring; 3, left auriculo-ventricular orifice, closed by the mitral valve; 4, fibrinous ring; 5, aortic orifice and valves; 6, pulmonic orifice and valves; 7, 8, 9, muscular fibres.

*Aortic Valves.*—These valves, also called the semilunar, or sigmoid valves of the left side, present no difference from the valves at the orifice of the pulmonary artery. They are situated at the aortic orifice.

## MOVEMENTS OF THE HEART.

The dilatation of the cavities of the heart is called the diastole, and the contraction of the heart, the systole. When these terms are used without any qualification, they are understood as referring to the ventricles; but they are also applied to the action of the auricles, as the auricular diastole and systole, which are distinct from the action of the ventricles.

A complete revolution of the heart consists in the filling and emptying of all its cavities, during which they present an alternation of repose and activity. As these phenomena occupy, in many warm-blooded animals, a period of time less than one second, it will be appreciated that the most careful study is necessary in order to ascertain their exact relations to each other. When the heart is exposed in a living animal, the most prominent phenomenon is the alternate contraction and relaxation of the ventricles; but this is only one of the operations of the organ. In all the mammalia, the anatomy and action of the vascular system are practically the same as in the human subject; and although the exposure of the heart by opening the chest modifies somewhat the force and frequency of its pulsations, the various phenomena follow each other in their natural order and present essentially their normal characters. Having opened the chest, keeping up artificial respiration, the heart, enveloped in its pericardium, is observed, contracting regularly; and on slitting up and removing this covering, the various parts are completely exposed. The right ventricle and auricle and a portion of the left ventricle can be seen without disturbing the position of the parts; but the greater part of the left auricle is concealed. As both auricles and ventricles act together, the parts of the heart which are exposed are sufficient for purposes of study.

*Action of the Auricles.*—Except the short time occupied in the contraction of the auricles, these cavities are continually receiving blood, on the right side from the general system, by the venæ cavæ, and on the left side from the lungs, by the pulmonary veins. This continues until the cavities of the auricles are completely filled, the blood coming in by a steady current; and during the repose of the heart, the blood is also flowing through the auriculo-ventricular orifices into the ventricles. When the auricles have become fully distended, they contract quickly and with considerable power (the auricular systole), and force the blood into the ventricles, producing complete diastole of these cavities. During this contraction, the blood not only ceases to flow in from the veins, but some of it is regurgitated, as the orifices by which the vessels open into the auricles are not provided with valves. The size of the auriculo-ventricular orifices is one reason why the greater portion of the blood is made to pass into the ventricles; and farthermore, during the auricular systole, the muscular fibres which are arranged around the orifices of the veins constrict them to a certain extent, which tends to diminish the reflux of blood. There can be no doubt that some regurgitation takes place from the auricles into the veins, but this prevents the possibility of over-distention of the ventricles.

It has been shown that the systole of the auricles is not immediately necessary to the performance of the circulation; and the contractility of the auricles may be temporarily exhausted by repeated and prolonged stimulation, the ventricles continuing to act, keeping up the circulation of blood.

*Action of the Ventricles.*—Immediately following the contraction of the auricles, by which the ventricles are completely distended, there is contraction of the ventricles. This is the chief active operation performed by the heart and is generally spoken of as the systole. The contraction of the ventricles is very much more powerful than that of the auricles. By their action, the blood is forced from the right side to the lungs, by the pulmonary artery, and from the left side to the general system, by the aorta. Regurgitation into the auricles is prevented by the closure of the tricuspid and mitral valves. This act accomplished, the heart has a period of repose, the blood flowing into the auricles, and from them into the ventricles, until the auricles are filled and another contraction takes place.

*Locomotion of the Heart.*—The position of the heart after death or during the repose of the organ is with its base directed slightly to the right and its apex to the left side of the body. With each ventricular systole, the apex is sent forward and is moved slightly from left to right. The movement from left to right is a necessary consequence of the course of the superficial fibres. The fibres on the anterior surface of the organ are longer than those on the posterior surface, and pass from the base, which is comparatively fixed, to the apex, which is immovable. As a consequence of this anatomical arrangement, the heart is moved upward and forward during its systole. The course of the fibres from the base to the apex is from right to left; and as they shorten, the apex is of necessity slightly moved from left to right.

The locomotion of the heart takes place in the direction of its axis and is due to the sudden distention of the great vessels at its base. These vessels are elastic, and as they receive the charge of blood from the ventricles, they become enlarged in every direction and consequently project the entire organ against the walls of the chest. This movement is aided by the recoil of the ventricles as they discharge their contents.

*Twisting of the Heart.*—The spiral course of the superficial fibres involves another phenomenon accompanying its contraction; namely, twisting. By attentively watching the apex, especially when the action of the heart is slow, there is observed a palpable twisting of the point upon itself from left to right with the systole, and an untwisting with the diastole.

*Hardening of the Heart.*—If the heart of a living animal be grasped by the hand, it will be observed that at each systole it becomes hardened. The fact that it is composed almost exclusively of fibres resembling very closely those of the voluntary muscles, explains this phenomonen. Like any other muscle, it is sensibly hardened during contraction.

*Shortening of the Ventricles.*—The point of the heart is protruded during the ventricular systole, but this protrusion is not due to elongation of the ventricles. By suddenly cutting the heart out of a warm-blooded animal and watching the phenomena which accompany the few regular movements which follow, it is seen that the ventricles invariably shorten as they contract. This can easily be appreciated by the eye, but more readily if the point of the organ be brought just in contact with a plane surface at a right angle, when, at each contraction, it is unmistakably observed to recede. During the intervals of contraction, the great vessels, particularly the aorta and pulmonary artery, which attach the base of the heart to the posterior wall of the thorax, are filled but not distended with blood; at each systole, however, these vessels are distended to their utmost capacity; their elastic coats admit of considerable enlargement, as can be seen in the living animal, and this enlargement, taking place in every direction, pushes the whole organ forward. It is for this reason that, in observing the heart *in situ*, the ventricles seem to elongate. It is only when the heart is firmly fixed or is contracting after it has been removed from the body, that the actual changes which occur in the length of the ventricles can be appreciated. During the systole, the ventricles are shortened and are narrowed in their transverse diameter, but their antero-posterior diameter is slightly increased.

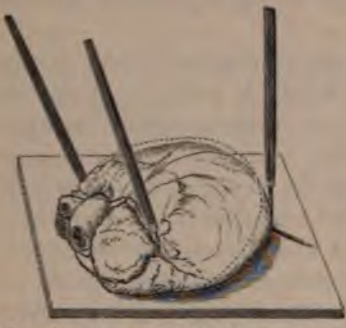

FIG. 19.—*Diagram of the shortening of the ventricles during systole.* The dotted lines show the position of the heart during contraction.

In addition to the marked changes in form, position etc., which the heart undergoes during its action, on careful examination it is seen that the surface of the ventricles becomes marked with slight, longitudinal ridges during the systole.

*Impulse of the Heart.*—Each movement of the heart produces an impulse, which can be readily felt and sometimes seen in the fifth intercostal space a little to the right of the perpendicular line of the left nipple. This impulse is synchronous with the contraction of the ventricles. If the hand be introduced into the chest of a living animal and the finger be placed between the point of the heart and the walls of the thorax, every time that there is a hardening of the point, the finger will be pressed against the side. If the impulse of the heart be felt while the finger is on the pulse, it is evident that the heart strikes against the thorax at the time of the distention of the arterial system. The impulse is due to the locomotion of the ventricles. In the words of Harvey, "the heart is erected, and rises upward to a point so that at this time it strikes against the breast and the pulse is felt externally."

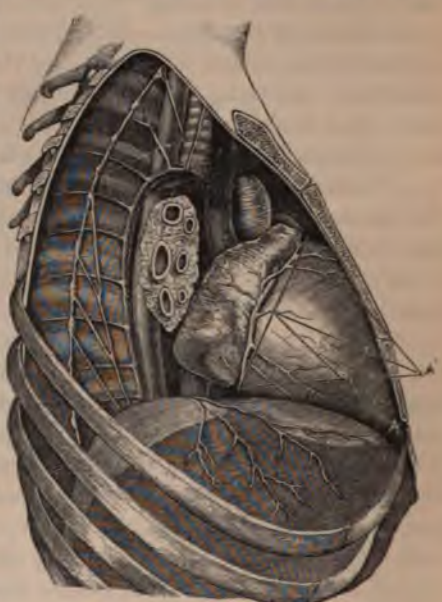

FIG. 20.—*Side view of the heart* (Landois). A, apex during diastole; A′, the same during systole. (Modified from Ludwig and Henke.)

*Succession of the Movements of the Heart.*—The main points in the succession of the movements of the heart are readily observed in cold-blooded animals, in which the pulsations are very slow. In examining the heart of the frog, turtle or alligator, the alternations of repose and activity are very strongly marked. During the intervals of contraction, the whole heart is flaccid and the ventricle is comparatively pale; the auricles then slowly fill with blood; when they have become fully distended, they contract and fill the ventricle, which in these animals is single; the ventricle immediately contracts, its action following upon the contraction of the auricles as if it were propagated from them. When the heart is filled with blood, it has a dark-red color, which contrasts strongly with its appearance after the systole. These phenomena may occupy ten to twenty seconds, giving an abundance of time for observation. The case is different, however, with the warm-blooded animals, in which the anatomy of the heart is nearly the same as in man. Here a normal revolution may occupy less than a second; and it is evident that the varied phenomena just mentioned are followed with more difficulty. In spite of this rapidity of action, it can be seen that a rapid contraction of the auricles precedes the ventricular systole, and that the latter is synchronous with the cardiac impulse.

The experiments of Marey, with reference to the relations between the systole of the auricles, the systole of the ventricles and the impulse of the heart, were performed upon horses, in the following way:

A sound is introduced into the right side of the heart through the jugular vein. This sound is provided with two initial bags, one of which is lodged in the right auricle, while the other passes into the ventricle. The bags are connected with distinct tubes which pass one within the other and are connected by elastic tubing with the registering apparatus. At each systole of the heart, the bags in its cavities are compressed and produce corresponding movements of the levers, which may be registered simultaneously.

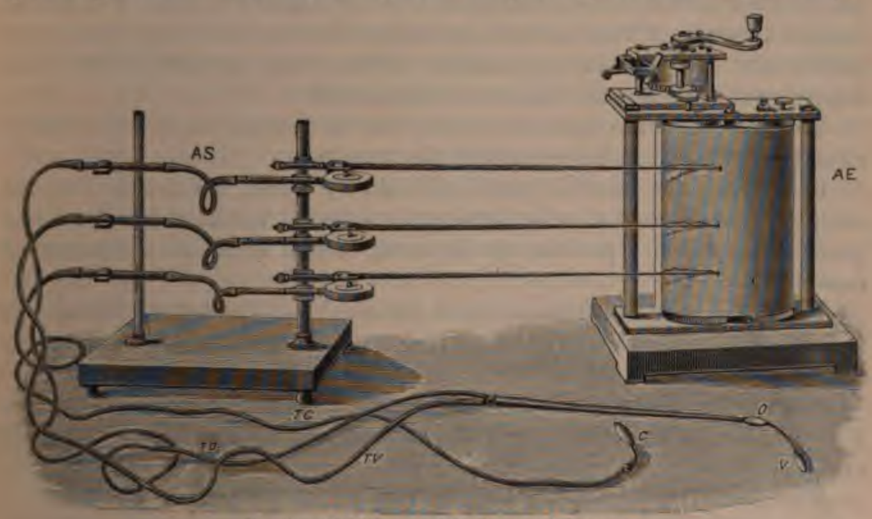


FIG. 21.—*Cardiograph* (Chauveau and Marey).

"The instrument is composed of two principal elements: A E, the registering apparatus, and A S, the sphygmographic apparatus, that is to say, which receives, transmits, and amplifies the movements which are to be studied." The compression exerted upon the bag *c*, which is placed over the apex of the heart, between the intercostal muscles, is conducted by the tube *t c*, which is filled with air, to the first lever. The compression exerted upon the bags *o* and *v*, in the double sound, is conducted by the tubes *t o* and *t v* to the two remaining levers. The movements of the levers are registered simultaneously by the cylinder A E.

To register the impulse of the heart, an incision is made through the skin and the external intercostal muscle over the point where the apex-beat is felt.

A little bag, stretched over two metallic buttons separated by a central rod, is then secured in the cavity thus formed and is connected by an elastic tube with the registering apparatus. All the tubes are provided with stop-cocks, so that each initial bag may be made to communicate with its lever at will. When the operation is completed and the sound is firmly secured in place by a ligature around the vein, the animal experiences no inconvenience, is able to walk about, eat etc., and there is every evidence that the circulation is not interfered with. The cylinder which carries the paper destined to receive the traces is arranged to move by clock-work at a given rate. The paper may also be ruled in lines, the distances between which represent certain fractions of a second. Fig. 21 represents the apparatus reduced to one-sixth of its actual size. Two of the levers are connected with the double sound for the right auricle and ventricle, and one is connected with the bag destined to receive the impulse of the heart. In an experiment upon a horse, the movements of the three levers produced traces upon the paper which were interpreted as follows:

The auricular systole, marked by the first lever, immediately preceded the ventricular systole and occupied about two-tenths of a second. The elevation of the lever indicated that it was much more feeble than the ventricular systole, and sudden in its character; the contraction, when it had arrived at the maximum, being immediately followed by relaxation.

The ventricular systole, marked by the second lever, immediately followed the auricular systole and occupied about four-tenths of a second. The almost vertical direction of the trace and the degree of elevation showed that it was sudden and powerful in its character. The abrupt descent of the lever showed that the relaxation was almost instantaneous.

The impulse of the heart, marked by the third lever, was shown to be absolutely synchronous with the ventricular systole.

Condensing the general results obtained by Marey, which are of course subject to some variation, and dividing the action of the heart into ten equal parts, three distinct periods are observed, which occur in the following order:

*Auricular Systole.*—This occupies two-tenths of the heart's action. It is feeble as compared with the ventricular systole, and relaxation immediately follows the contraction.

*Ventricular Systole.*—This occupies four-tenths of the heart's action. The contraction is powerful and the relaxation is sudden. It is absolutely synchronous with the impulse of the heart.

*Auricular Diastole.*—This occupies four-tenths of the heart's action.

*Force of the Heart.*—Hales (1733) was the first to investigate experimentally the question of the force exerted by the heart, by the application of the cardiometer. He showed that the pressure of blood in the aorta could be measured by the height to which the fluid would rise in a tube connected with that vessel, and estimated the force of the left ventricle by multiplying the pressure in the aorta by the area of the internal surface of the ventricle. The cardiometer has since undergone various improvements and modifications, but the above is the principle made use of at the present day in estimating the pressure of the blood in different parts of the circulatory system.

Hales estimated, from experiments upon living animals, the height to which the blood would rise in a tube connected with the aorta of the human subject, at 7 feet 6 inches (228·6 centimetres), and gave the area of the left ventricle as 15 square inches (96·67 square centimetres). From this he calculated the force of the left ventricle as equal to 51·5 pounds (about 23 kilos.). Although this estimate is merely an approximation, it seems to be based on more reasonable data than any other.

The apparatus of Marey for registering the contractions of the different cavities of the heart enabled him to ascertain the comparative force of the two ventricles and the right auricle; the situation of the left auricle precluding the possibility of introducing a sound into its cavity. By first subjecting the bags to known degrees of pressure, the line of elevation of a lever may be graduated so as to represent the degrees of the cardiometer. In analyzing traces made by the left ventricle, the right ventricle and right auricle, in the horse, Marey found that as a general rule, the comparative force of the right and left ventricles is as one to three. The force of the right auricle is comparatively insignificant, being in one case, as compared with the right ventricle, only as one to ten.

*Action of the Valves.*—In man and the warm-blooded animals, there are no valves at the orifices by which the veins open into the auricles. As has already been seen, compared with the ventricles, the force of the auricles is insignificant; and it has farthermore been shown that the ventricles may be filled with blood and the circulation continue when the auricles are entirely passive. Although the orifices are not provided with valves, the circular arrangement of the fibres about the veins is such, that during the contraction of the auricles the openings are considerably narrowed and regurgitation can not take place to any great extent. The force of the blood flowing into the auricles likewise offers an obstacle to its return. There is really no valvular apparatus which operates to prevent regurgitation from the heart into the veins; for the valvular folds, which are so abundant in the general venous system and particularly in the veins of the extremities, do not exist in the venæ cavæ. The continuous flow of blood from the veins into the auricles, the feeble character of the auricular contractions, the arrangement of the fibres around the orifices of the vessels, and the great size of the auriculo-ventricular openings, are conditions which provide sufficiently for the flow of blood into the ventricles.

*Action of the Auriculo-Ventricular Valves.*—After the ventricles have become completely distended by the auricular systole, they take on their contraction, which is very many times more powerful than the contraction of the auricles. They force open the valves which close the orifices of the pulmonary artery and aorta and empty their contents into these vessels. To accomplish this, at the moment of the ventricular systole, there is a complete closure of the auriculo-ventricular valves, leaving only the auriculo-ventricular opening through which the blood can pass. That these valves close at the moment of contraction of the ventricles, was demonstrated by the experiments of Chauveau and Faivre, who introduced the finger through an opening into the auricle and actually felt the valves close at the instant of the ventricular systole. This tactile demonstration, and the fact that the first sound of the heart, which is produced in part by the closure of the auriculo-ventricular valves, is synchronous with the ventricular systole, leave no doubt as to the mechanism of the closure of these valves. It is probable that as the blood flows into the ventricles, the valves are slightly floated out, but they are not closed until the ventricles contract.

If a bullock's heart be prepared by cutting away the auricles so as to expose the mitral and tricuspid valves, securing the nozzles of a double syringe in the pulmonary artery and aorta after having destroyed the semilunar valves, and if fluid be injected simultaneously into both ventricles, the play of the valves will be exhibited. The mitral valve effectually prevents the passage of fluid, its edges being so accurately adapted that not a drop passes between them; but when the pressure is considerable, a certain quantity of fluid passes the tricuspid valve (T. W. King). There is, indeed, a certain degree of insufficiency of the tricuspid valve, which does not exist on the opposite side; but it is very questionable whether there can be sufficient force exerted by the right ventricle to produce regurgitation of blood at the right auriculo-ventricular orifice.

*Action of the Aortic and Pulmonic Valves.*—The action of the semilunar valves is nearly the same upon both sides. In the intervals of the ventricular contractions, they are closed and prevent regurgitation of blood into the ventricles. The systole, however, overcomes the resistance of these valves and forces the contents of the ventricles into the arteries. During this time, the valves are applied, or nearly applied, to the walls of the vessel; but so soon as the ventricles cease their contraction, the constant pressure of the blood, which is very great, closes the openings.

The action of the semilunar valves can be studied by cutting away a portion of the ventricles in the heart of a large animal, securing the nozzles of a double syringe in the aorta and pulmonary artery and forcing water into the vessels. It has been observed that while the aortic semilunar valves oppose the passage of the liquid so effectually that the aorta may be ruptured before the valves will give way, a certain degree of insufficiency exists, under a high pressure, at the orifice of the pulmonary artery (Flint, 1864). A slight insufficiency of the pulmonic valves was observed by John Hunter, in 1794. It is not probable, however, that the pressure of blood in the pulmonary artery is ever sufficient to produce regurgitation when the valves are normal.

It is probable that the corpuscles of Arantius, which are situated in the middle of each valvular curtain, assist in the accurate closure of the orifice. The sinuses of Valsalva, situated in the artery behind the valves, are regarded as facilitating the closure of the valves by allowing the blood to pass easily behind them.

*Sounds of the Heart.*—The appreciable phenomena which attend the heart's action are connected with the systole of the ventricles. It is this which produces the impulse against the walls of the thorax, and as will be seen farther on, the dilatation of the arterial system, indicated by the pulse. It is natural, therefore, in studying these phenomena, to take the systole as a point of departure, instead of the action of the auricles; and the sounds, which are two in number, have been called first and second, with reference to the ventricular systole.

The first sound is absolutely synchronous with the apex-beat. The second sound follows the first with scarcely an appreciable interval. Between the second and the first sound, there is an interval of silence.

Some writers have attempted to represent the sounds of the heart and their relations to each other, by certain syllables, as "*lubb-dup* or *lubb-tub*"; but it seems unnecessary to attempt to make such a comparison, which can only be appreciated by one who is practically acquainted with the heart-sounds, when the sounds themselves can be so easily studied.

Both sounds are generally heard with distinctness over the entire præcordial region. The first sound is heard with its maximum of intensity over the body of the heart, a little below and within the nipple, between the fourth and fifth ribs, and is propagated with greatest intensity downward, toward the apex. The second sound is heard with its maximum of intensity at the base of the heart, between the nipple and the sternum, at about the third rib, and is propagated upward, along the course of the great vessels. If the stethoscope be placed between the point of the apex-beat and the left nipple, the first sound will be heard strongly accentuated, and presenting a certain quality in its valvular element, due to the closure of the mitral valve. If the stethoscope be then removed to a point a little to the left of the ensiform cartilage, the element due to the closure of the tricuspid valve will predominate, and a slight but distinct difference in quality may frequently be noted. An analogous difference in the valvular elements of the second sound may also be observed. When the stethoscope is placed at the base of the heart, just to the right of the sternum and over the aortic valves, the character of the second sound is often notably different from the character of the sound heard with the stethoscope placed just to the left of the sternum, over the pulmonic valves. In this way the valvular elements of the two sounds of the heart may be separated, each one into two, one produced by closure of the valves on the left side, and one by closure of the valves of the right side. A recognition of these nice distinctions is useful in physical examinations of the heart in disease.

The rhythm of the sounds bears a definite relation to the rhythm of the heart's action. Laennec was the first to direct special attention to the rhythm of the heart-sounds, although the sounds themselves were recognized by Harvey, who compared them to the sounds made by the passage of fluids along the œsophagus of a horse when drinking. Laennec divided a single revolution of the heart into four equal parts: the first two parts, occupied by the first sound; the third part, by the second sound; and the fourth part, with no sound. He regarded the second sound as following immediately after the first. Some authors have described a "short silence" as occurring after the first sound, and a "long silence," after the second sound. The short silence, if appreciable at all, is so indistinct that it may practically be disregarded.

Most physiologists regard the duration of the first sound as a little less than two-fourths of the heart's action, and the second sound as a little more than one-fourth. When the mechanism of the production of the two sounds is considered, it will be seen that if the views on that point be correct, the first sound should occupy the period of the ventricular systole, or four-tenths of the heart's action. The second sound occupies about three-tenths, and the repose, three-tenths.

The first sound is relatively dull, low in pitch, and is made up of two elements; one, a valvular element, in which it resembles in character the second sound, and the other, an element which is directly due to the action of the heart as a muscle. It has been ascertained that all muscular contraction is attended with a certain sound. To this is added an impulsion element, which is produced by the striking of the heart against the walls of the thorax.

The second sound is relatively sharp, high in pitch, and has but one element, which is purely valvular.

*Causes of the Sounds of the Heart.*—There is now scarcely any difference of opinion with regard to the cause of the second sound of the heart. The experiments of Rouanet (1832) settled beyond a doubt that it is due to closure of the aortic and pulmonary semilunar valves. In these experiments, the second sound was imitated by producing sudden closure of the aortic valves by a column of water. In the experiments of the British Commission, the semilunar valves were caught up by curved hooks introduced through the vessels of a living animal (the ass), with the result of abolishing the second sound and substituting for it a hissing murmur. When the instruments were withdrawn and the valves permitted to resume their action, the normal sound returned.

The cause of the first sound of the heart has not been so well understood. It was maintained by Rouanet that this sound was produced by the closure of the auriculo-ventricular valves; but the situation of these valves rendered it difficult to demonstrate this by actual experiment. While the second sound is purely valvular in its character, the first sound is composed of a certain number of different elements; but auscultatory experiments have been made by which all but the valvular element are eliminated, when the first sound assumes a purely valvular quality. These observations were made in 1858 by the late Dr. Austin Flint:

If a folded handkerchief be placed between the stethoscope and integument, the first sound is divested of some of its most distinctive features. It loses the quality of impulsion and presents a well marked valvular quality.

In many instances, when the stethoscope is applied to the præcordia while the subject is in a recumbent posture and the heart is removed by force of gravity from the anterior wall of the thorax, the first sound becomes purely valvular in character and as short as the second.

When the stethoscope is applied to the chest a little distance from the point where the first sound is heard with its maximum of intensity, it presents only its valvular element.

These observations, taken in connection with the fact that the first sound occurs when the ventricles contract and necessarily accompanies the closure of the auriculo-ventricular valves, show that these valves produce at least one element of the sound. In farther support of this opinion, is the fact that the first sound is heard with its maximum of intensity over the site of the valves and is propagated downward along the ventricles, to which the valves are attached. Actual experiments are not wanting to confirm this view. Chauveau and Faivre succeeded in abolishing the first sound by the introduction of a wire ring into the auriculo-ventricular orifice through a little opening in the auricle, so as to prevent the closure of the valves. When this is done, the first sound is lost; but on taking it out of the opening, the sound returns. These observers also abolished the first sound by introducing a small curved tenotomy-knife through the auriculo-ventricular orifice and dividing the chordæ tendineæ. In this experiment a loud rushing murmur took the place of the sound. These observations and experiments seem to settle the fact that the closure of the auriculo-ventricular valves produces one element of the first sound.

The other elements which enter into the composition of the first sound are not so prominent as the one just mentioned, although they serve to give it its prolonged and "booming" character. These elements are a sound like that produced by any large muscle during its contraction, called by some the muscular murmur, and the sound produced by the impulse of the heart against the walls of the chest.

There can be no doubt that the muscular murmur is one of the elements of the first sound; and it is this which gives to the sound its prolonged character when the stethoscope is applied over the body of the organ, as the sound produced in muscles continues during the whole period of their contraction. Admitting this to be an element of the first sound, its duration must necessarily coincide with that of the ventricular systole.

The impulse of the heart against the walls of the thorax also has a share in the production of the first sound. This is demonstrated by noting the difference in the sound when the subject is lying upon the back, and when he is upright, by interposing any soft substance between the stethoscope and the chest, or by auscultating the heart after the sternum has been removed. Under these conditions, the first sound loses its booming character, retaining, however, the muscular element when the instrument is applied to the exposed organ.

The observations showing the valvular character of one of the elements of the first sound have been so definite and positive in their results that one can hardly regard them as entirely controverted by the recent experiments (1885) of Yeo and Barrett, upon the hearts, cut from the body, of cats and dogs, which show, it is claimed, that "a definite and characteristic tone similar in quality to the first sound is produced by the heart-muscle under circumstances that render it impossible for any tension of the valves to contribute to its production." It will be assumed, therefore, that the sounds of the heart have a mechanism that may be summarized as follows:

The first sound of the heart is a compound sound. It is produced by the closure of the auriculo-ventricular valves at the beginning of the ventricular systole, to which are superadded, the muscular sound, due to the contraction of the muscular fibres of the heart, and the impulsion-sound, due to the striking of the heart against the walls of the thorax.

The second sound is a simple sound. It is produced by the sudden closure of the aortic and pulmonic semilunar valves, immediately following the ventricular systole.

It is of importance, with reference to pathology, to have a clear idea of the currents of blood through the heart, with their exact relations to the sounds and intervals. At the beginning of the first sound, the blood is forcibly thrown from the ventricles into the pulmonary artery on the right side and the aorta on the left, and the auriculo-ventricular valves are closed. During the period occupied by this sound, the blood is flowing through the arterial orifices, and the auricles are receiving blood slowly from the venæ cavæ and the pulmonary veins. When the second sound occurs, the ventricles having become relaxed, the recoil of the arterial walls, acting upon the column of blood, immediately closes the semilunar valves upon the two sides. The auricles continue to dilate, and the ventricles are slowly receiving blood. Immediately following the second sound, during the first part of the interval, the auricles become fully dilated; and in the last part of the interval, immediately preceding the first sound, the auricles contract and the ventricles are fully dilated, This completes a single revolution of the heart.

*Frequency of the Heart's Action.*—The number of pulsations of the heart is not far from seventy per minute in an adult male and is between seventy and eighty in the female. There are individual cases, however, in which the pulse is normally much slower or more frequent than this, a fact which must be remembered when examining the pulse in disease. It is said that the pulse of Napoleon I. was only forty per minute. Dunglison mentioned a case which came under his own observation, in which the pulse presented an average of thirty-six per minute. The same author stated that the pulse of Sir William Congreve was never less than one hundred and twenty-eight per minute, in health. It is by no means unfrequent to find a healthy pulse of a hundred or more a minute; but in the cases reported in which the pulse has been found to be forty or less, it is possible that every alternate beat of the heart was so feeble as to produce no perceptible arterial pulsation. In such instances, the fact may be ascertained by listening to the heart while the finger is placed upon the artery.

*Influence of Age and Sex.*—In both the male and female, observers have constantly found a great difference in the rapidity of the heart's action at different periods of life. The pulsations of the heart in the fœtus are about 140 per minute. At birth the pulse is 136. It gradually diminishes during the first year to about 128. The second year, the diminution is quite rapid, 107 being the mean frequency at two years of age. After the second year, the frequency progressively diminishes until adult life, when it is at its minimum, which is about 70 per minute. At the later periods of life the movements of the heart become slightly accelerated, ranging between 75 and 80 (Guy).

During early life there is no marked and constant difference in the rapidity of the pulse in the sexes; but near the age of puberty, the development of the peculiarities relating to sex is accompanied with an acceleration of the heart's action in the female, which continues even into old age.

*Influence of Digestion.*—The condition of the digestive system has a marked influence on the rapidity of the pulse, and there is generally an increase in the pulse of between five and ten beats per minute after each meal. Prolonged fasting diminishes the frequency of the pulse by about twelve beats. Alcohol first diminishes and afterward accelerates the pulse. Coffee is said to accelerate the pulse in a marked degree. It has been ascertained that the pulse is accelerated to a greater degree by animal than by vegetable food.

*Influence of Posture and Muscular Exertion.*—It has been observed that the position of the body has a very marked influence upon the rapidity of the pulse. In the male, there is a difference of about ten beats between standing and sitting, and fifteen beats between standing and the recumbent posture. In the female, the variations with position are not so great. The average is, for the male standing, 81; sitting, 71; lying, 66;—for the female: standing, 91; sitting, 84; lying, 80. This is given as the average of a large number of observations. There were a few instances, however, in which there was scarcely any variation with posture, and some in which the variation was much greater than the average. In the inverted posture, the pulse was found to be reduced about fifteen beats (Guy).

The question at once suggests itself whether the acceleration of the pulse in sitting and standing may not be due, in some measure, to the muscular effort required in making the change of posture. This is answered by the experiments of Guy, in which the subjects were placed on a revolving board and the position of the body was changed without any muscular effort. The same results as those cited above were obtained in these experiments, showing that the difference is due to the position of the body alone. In a single observation, the pulse, standing, was 89; lying, 77; difference, 12. With the posture changed without any muscular effort, the results were as follows: standing, 87; lying, 74; difference, 13. Different explanations of these variations have been offered by physilogists; but Guy seems to have settled experimentally the fact that the acceleration is due in part to the muscular effort required to maintain the body in the sitting and standing positions. The following are the results of experiments bearing on this point, in which it is shown that when the body is carefully supported in the erect or sitting posture, so as to be maintained without muscular effort, the pulse is less frequent than when the subject is standing; and farthermore, that the pulse is accelerated, in the recumbent posture, when the body is imperfectly supported :

"1. Difference between the pulse in the erect posture, without support, and leaning in the same posture, in an average of twelve experiments on the writer, 12 beats; and on an average of eight experiments on other healthy males, 8 beats.

"2. Difference in the frequency of the pulse in the recumbent posture, the body fully supported, and partially supported, 14 beats on an average of five experiments.

"3. Sitting posture (mean of ten experiments on the writer), back supported, 80; unsupported, 87; difference, 7 beats.

"4. Sitting posture with the legs raised at right angles with the body (average of twenty experiments on the writer), back unsupported, 86; supported, 68; difference, 18 beats. An average of fifteen experiments of the same kind on other healthy males gave the following numbers: back unsupported, 80; supported, 68; a difference of 12 beats."

*Influence of Exercise etc.*—Muscular exertion increases the frequency of the pulsations of the heart; and the experiments just cited show that the difference in rapidity, which is by some attributed to change in posture—some positions, it is fancied, offering fewer obstacles to the current of blood than others—is mainly due to muscular exertion. According to Bryan Robinson (1734), a man in the recumbent position has 64 pulsations per minute; sitting, 68; after a slow walk, 78; after walking four miles in an hour, 100; and 140 to 150 after running as fast as he could. This general statement, which has been repeatedly verified, shows the important influence of the muscular system on the heart.

The influence of sleep upon the action of the heart reduces itself almost entirely to the proposition that during this condition, there is usually entire absence of muscular effort, and consequently the number of beats is less than when the individual is aroused. It has been found that there is no difference in the pulse between sleep and perfect quiet in the recumbent posture. This fact obtains in the adult male; but there is a marked difference in females and young children, the pulse being always slower during sleep (Quetelet).

*Influence of Temperature.*—The influence of extremes of temperature upon the heart is very decided. The pulse may be doubled by remaining a very few minutes exposed to extreme heat. Bence Jones and Dickinson have ascertained that the pulse may be very much reduced in frequency, for a short time, by the cold douche. It has also been remarked that the pulse is habitually more rapid in warm than in cold climates.

Although many circumstances materially affect the rapidity of the heart's action, they do not complicate, to any great extent, examinations of the pulse in disease. In cases which present considerable febrile movement, the patient is generally in the recumbent posture. The variations induced by violent exercise are easily recognized, while those dependent upon temperature, the condition of the digestive system, etc., are so slight that they may practically be disregarded. It is necessary to bear in mind, however, the variations which exist in the sexes and at different periods of life, as well as the possibility of individual peculiarities, when the action of the heart is extraordinarily rapid or slow.

*Influence of Respiration upon the Action of the Heart.*—The relations between the circulation and respiration are very intimate and one process can not go on without the other. If circulation be arrested, the muscles, being no longer supplied with fresh blood, soon lose their contractile power, and respiration ceases. Circulation, also, is impossible if respiration be permanently arrested. When respiration is imperfectly performed, the action of the heart is slow and labored. The effects of arrest of respiration are marked in all parts of the circulatory system, arteries, capillaries and veins; but the disturbances thus produced all react upon the heart.

If the heart be exposed in a living animal and artificial respiration be kept up, although the pulsations are increased in frequency and diminished in force, after a time they become perfectly regular and continue thus so long as air is adequately supplied to the lungs. Under these conditions, respiration is entirely under control and the effects of its arrest upon the heart can easily be studied. If respiration be interrupted, the following changes in the action of the heart are observed: For a few seconds pulsations go on as usual, but in about a minute they begin to diminish in frequency. At the same time, the heart becomes engorged with blood and the distention of its cavities rapidly increases. For a time its contractions are competent to discharge the entire contents of the left ventricle into the arterial system, and a cardiometer applied to an artery will indicate a great increase in the pressure of blood. A corresponding increase in the movements of the mercury will be noted at each contraction of the heart, indicating that the organ is acting with abnormal vigor. If respiration be still interrupted, the engorgement becomes intense, the heart at each diastole being distended to its utmost capacity. It now becomes incapable of emptying itself, the contractions become very unfrequent, perhaps three or four in a minute, and are progressively enfeebled. The organ is dark, almost black, owing to the circulation of venous blood in its substance. If respiration be not resumed, this distention continues, the contractions become less frequent and more feeble, and in a few minutes they cease.

The arrest of the action of the heart, under these conditions, is chiefly mechanical. The unaërated blood passes with difficulty through the capillaries of the system, and as the heart is constantly at work, the arteries become largely distended. This is shown by the great increase in the arterial pressure while these vessels are full of black blood. If, now, the heart and great vessels be closely examined, the order in which they become distended is readily observed. These phenomena show that in asphyxia the obstruction to the circulation begins, not in the lungs, as is commonly supposed, but in the capillaries of the system, and is propagated backward to the heart through the arteries (Dalton). The distention of the heart in asphyxia is therefore due to the fact that unaërated blood can not circulate freely in the systemic capillaries. When thus distended, the heart becomes paralyzed, like any muscle after a severe strain.

If respiration be resumed before the heart's action has entirely ceased, the organ in a few moments will resume its contractions. There is observed first a change from the dusky hue it had assumed, to a vivid red, which is owing to the circulation of arterial blood in its capillaries. The distention then becomes gradually relieved, and for a few moments, the pulsations are abnormally frequent. The arteries will then be found to contain red blood. An instrument applied to an artery will show a diminution in arterial pressure and in the force of the heart's action, if the arrest of respiration have been carried only far enough to moderately distend the heart; or there is an increase in the pressure and force of the heart, if its action have been nearly arrested. A few moments of regular insufflation will cause the pulsations to resume their normal character and frequency.

In the human subject, the effects of temporary or permanent arrest of respiration on the heart are undoubtedly the same as those observed in experiments upon the warm-blooded animals. In the same way, also, it is possible to restore the normal action of the organ, if respiration be not too long suspended, by the regular introduction of fresh air into the lungs. Examples of animation restored by artificial respiration, in drowning etc., are evidence of this fact. In cases of asphyxia, those measures by which artificial respiration is most effectually maintained have been found most efficient.

### Cause of the Rhythmical Contractions of the Heart.

The question of the actual cause of the rhythmical contractions of the heart is one of great importance and has long engaged the attention of physiologists. While researches have resulted in much positive information with regard to influences which regulate or modify this action, there seems to be little known, even now, concerning the main question, why the fibres of the heart, unlike the ordinary muscular fibres, seem to contract spontaneously.

The heart in its structure resembles the voluntary muscles; but it has a constant office to perform and seems to act without any palpable excitation, while the latter act only under the influence of a natural stimulus, like the nervous impulse, or under artificial excitation. The movements of the heart are not the only examples of what seems to be spontaneous action. The ciliated epithelium is in motion from the beginning to the end of life, and will continue for a certain time, even after the cells are detached from the organism. This motion can not be explained, unless it be called an explanation to say that it is dependent upon vital properties; but if the actual cause of the rhythmical contraction of the heart be unknown, physiologists are acquainted with certain influences which render its action regular, powerful and sufficient for the purposes of the economy.

The action of the heart is involuntary. Its pulsations can be neither arrested, retarded nor accelerated by an effort of the will, excepting, of course, examples of arrest by stoppage of respiration or acceleration by violent muscular exercise etc. In this respect the heart differs from certain muscles, like the muscles of respiration, which act automatically, but the movements of which may be temporarily arrested or accelerated by a direct voluntary effort. The last-mentioned fact illustrates the difference between the heart and all other striated muscles. All of them, in order to contract, must receive a stimulus, either natural or artificial. The natural stimulus comes from the nerve-centres and is conducted by the nerves. If the nerves going to any of the respiratory muscles, for example, be divided, the muscle is paralyzed and will not contract without some kind of stimulation. Connection with the central nervous system does not seem necessary to the action of the heart, for it will contract, especially in the cold-blooded animals, some time after its removal from the body. If the supply of blood be cut off from the substance of the heart, especially in the warm-blooded animals, the organ soon loses its contractility.

Erichsen, after exposing the heart in a warm-blooded animal and keeping up artificial respiration, tied the coronary arteries, thus cutting off the greatest part of the supply of blood to the muscular fibres. He found, as the mean of six experiments, that the heart ceased pulsating, although artificial respiration was continued, in twenty-three and a half minutes. After the pulsations had ceased, they could be restored by removing the ligatures and allowing the blood to circulate again in the substance of the heart.

The regular and powerful contractions of the heart are promoted by the circulation of the blood through its cavities. Although the heart, removed from the body, will contract for a time without a stimulus, it can be made to contract during the intervals of repose by an irritant, such as the point of a needle or a feeble electric current. For a certain time after the heart has ceased to contract spontaneously, contractions may be produced in this way. This can easily be demonstrated in the heart of any animal, warm-blooded or cold-blooded. This excitability, which is manifested, under these conditions, in the same way as in ordinary muscles, is different in degree in different parts of the organ. Haller and others have shown that it is greater in the cavities than on the surface; for long after stimulation applied to the exterior fails to excite contraction, the organ will respond to a stimulus applied to its interior. The experiments of Haller also show that fluids in the cavities of the heart have an influence in exciting and keeping up its contractions. This observation is important, as showing that the presence of blood is necessary to the natural and regular action of the heart. Schiff succeeded in restoring the pulsations in the heart of a frog, which had ceased after it had been emptied, by introducing a few drops of blood into the auricle. Experiments upon alligators and turtles show that when the heart is removed from the body and emptied of blood, the pulsations are feeble, rapid and irregular; but when filled with blood, the valves being destroyed so as to allow free passage in both directions between the auricles and ventricle, the contractions become powerful and regular. In these experiments, when water was introduced instead of blood, the pulsations were more frequent and not so powerful as when blood was used (Flint, 1861). These experiments show, also, that the action of the heart may be affected by the character, particularly the density, of the fluid which passes through its cavities, which may explain its rapid and feeble action in certain cases of anæmia. The heart, therefore, although capable of independent action, is excited to contraction by the blood as it passes through its cavities. A glance at the succession of its movements, particularly in cold-blooded animals—in which they are so slow that the phenomena can be easily observed—will show how these contractions are produced. There is first a distention of the auricle, and this is immediately followed by a contraction filling the ventricle, which in its turn contracts. Undoubtedly, the tension of the fibres, as well as the contact of blood in its interior, acts as a stimulus; and as all the fibres of each cavity are put on the stretch at the same instant, they contract simultaneously. The successive and regular distention of each cavity thus produces rhythmical and forcible contractions; and the mere fact that the action of the heart alternately empties and dilates its cavities insures regular pulsations, so long as blood is supplied and no disturbing influences are in operation.

The intermittent contraction and successive action of the fibres of the heart, when the organ has been removed from the body, are dependent, to a great extent, upon sympathetic ganglia situated near its base. If the ventricle of a frog's heart be divided transversely at the upper third, the lower two-thirds will no longer contract spontaneously, while the auricles and the upper third of the ventricle continue to pulsate. If a stimulus be then applied to the lower two-thirds of the ventricle, this is usually followed by a single contraction, and not by a series of more or less regular pulsations. It has been observed, also, that small, detached pieces of the auricles will pulsate regularly for a time.

In the frog there are three ganglia closely connected with the heart; one at an expansion of the inferior vena cava just before it enters the auricle, called the venous sinus (Remak), another between the left auricle and the ventricle (Bidder), and a third between the two auricles (Ludwig). According to Robert Meade Smith, the first two ganglia communicate the motor impulse to the muscular fibres of the heart. The third is the inhibitory ganglion, and this regulates, through its action upon the motor ganglia, the transmission of motor impulses. "As regards the manner in which these ganglia produce the *rhythmical* contraction of the heart, little is known; but that they are the prime factors in producing not only the rhythm of the cardiac revolutions, with its various modifications, but also the starting point of each individual contraction, is one of the best established facts in physiology."

In man and in most warm-blooded animals, collections of sympathetic ganglia are found attached to the nerves at the line of junction of the auricles with the ventricles.

Nearly all of the experiments just referred to were made upon the hearts of cold-blooded animals, particularly the frog; but in all animals, under normal conditions, the contractions of the heart seem to start from the auricles. The fact, however, that the ventricles will contract regularly in a living animal, after the excitability of the auricles has been exhausted by repeated stimulations and they have ceased to pulsate, shows that the so-called pulsating wave coming from the auricles is not absolutely essential to the contraction of the ventricles.

Finally, in view especially of the results of experiments upon the cold-blooded animals, it may be stated that the muscular fibres of the auricles and of the upper third of the ventricles have the property of intermittent and regular contraction, which is dependent, to a great extent, upon the influence of the so-called motor ganglia of the heart; and that the wave of contraction is transmitted to the lower two-thirds of the ventricles, the fibres of which do not seem to possess the property of independent contraction. The muscular tissue of the heart, however, may be thrown into contraction during diastole by the application of a stimulus, a property which is observed in all musular fibres. The excitability manifested in this way is much more marked in the interior than on the exterior of the organ. Blood in contact with the lining membrane of the heart acts as a stimulus in a remarkable degree and is even capable of restoring excitability after it has become extinct. The passage of blood through the heart is the natural stimulus of the organ and is an important element in the production of regular pulsations, although it by no means endows the fibres with their contractile properties.

*Accelerator Nerves.*—Experiments on the influence of the sympathetic nerves upon the heart have not been entirely satisfactory. It has been observed that the action of the heart is immediately arrested by destroying the cardiac plexus; but with regard to this, the difficulty of making the operation and the disturbance of the heart consequent upon the necessary manipulations must be taken into account. It has been shown, however, that stimulation of the sympathetic in the neck has the effect of accelerating the cardiac movements.

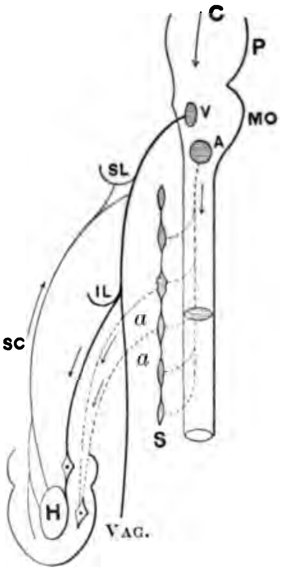


FIG. 22.—*Scheme of the course of the accelerans fibres* (Stirling).
P, pons; MO, medulla oblongata; V, inhibitory centre for the heart; A, accelerans centre; VAG., vagus; SL, superior, IL, inferior laryngeal; SC, superior cardiac; H, heart; C, cerebral impulse; S, cervical sympathetic; *a*, *a*, accelerans fibres.

According to Stricker, there exists in the medulla oblongata a centre, stimulation of which increases the rapidity of the heart's action; and from this centre, fibres descend in the substance of the spinal cord, pass out with the communicating branches of the lower cervical and upper dorsal nerves to the sympathetic, and go to the cardiac plexus. In the cat, the accelerator fibres pass through the first thoracic sympathetic ganglion. Taking all precautions to eliminate the influence of variations in the blood pressure, it has been shown that after division of the pneumogastric, stimulation of the accelerator fibres increases the number of beats of the heart. This action is direct and not reflex.

*Direct Inhibition of the Heart.*—Division of the pneumogastric nerves in the neck increases the frequency and diminishes the force of the contractions of the heart. To anticipate a little of the history of the pneumogastric nerves, it may be stated that while they are exclusively sensory at their origin, they receive, after having emerged from the cranial cavity, a number of filaments from various motor nerves. That they influence certain muscles, is shown by the paralysis of these muscles after division of the nerves in the neck, as, for example, the arrest of the movements of the glottis.

A moderate Faradic current passed through both pneumogastrics arrests the action of the heart in diastole (Ed. Weber). This observation has been made upon living animals, both with and without exposure of the heart; and this kind of action is known as inhibitory, or restraining. Its nervous mechanism is direct and not reflex; and the inhibitory influence is conveyed to the heart through filaments in the pneumogastric which are derived from the spinal accessory.

It is said that direct stimulation of the medulla oblongata will have the same effect upon the heart as stimulation of the pneumogastrics; but it must be very difficult to limit the stimulation to a particular point in the medulla and to avoid conditions which would complicate such an experiment. A sufficiently powerful stimulus applied to one pneumogastric will arrest the cardiac pulsations, and in some animals the inhibitory action is confined to the nerve of the right side. It is not known that any such difference between the two nerves exists in the human subject, and certainly there is no marked difference in most of the mammalia.

If both pneumogastrics be Faradized for two or three minutes, the contractions of the heart return, even though the stimulation be continued, provided the current be not too powerful but of sufficient strength to promptly arrest the pulsations. It is probable that this is due to the fact that the excitability of the nerve after a time becomes exhausted by the prolonged excitation, and its inhibitory influence is for the time destroyed.

Stimulation of the pneumogastrics in any part of their course is followed by the usual inhibitory phenomena, and the same results sometimes follow stimulation of the thoracic cardiac branches. It has also been observed that when the heart's action has been arrested and the organ is quiescent in diastole, direct mechanical stimulation of the heart is followed by a single contraction, showing that the excitability of the fibres has not been entirely suspended.

After section of both pneumogastrics in the neck, digitalis fails to diminish the number of beats of the heart (Traube); showing that separation of the heart from its connections with the cerebro-spinal nerves removes the organ from the characteristic and peculiar effects of the poison.

Feeble stimulation of one or both pneumogastrics, when it produces any effect, almost always slows the action of the heart. In some animals, however, the pneumogastrics contain a few accelerator fibres, and feeble excitation sometimes is followed by a slight increase in the rapidity of the cardiac pulsations, but this is unusual.

*Reflex Inhibition of the Heart.*—Like most of the direct operations of nerves that can be imitated by electric stimulation, the inhibitory action of the pneumogastrics can be produced by reflex action. The action of the heart may be arrested in the frog by sharply tapping the exposed intestines (Goltz). The same effect has been produced by stimulation of the splanchnic nerves or the cervical sympathetic. In some animals, if one pneumogastric be divided in the neck, the other being left intact, stimulation of the central end of the divided nerve will produce inhibition of the heart, by an action induced in the undivided nerve. In all of these instances, the inhibition is reflex. The stimulation is carried by the afferent fibres of the nerves stimulated, to the inhibitory centre in the medulla oblongata, and is reflected to the heart through the efferent fibres of the pneumogastric.

While moderate stimulation of ordinary sensory nerves is sometimes followed by inhibition of the heart, very powerful stimulation arrests the cardio-inhibitory action of the pneumogastrics, as well as certain other reflexes.

The inhibitory fibres of the pneumogastrics undoubtedly have an important office in connection with the regulation of the rapidity and force of the cardiac pulsations. It is important, of course, that the heart should act at all times with nearly the same force and frequency. It has been seen that the inherent properties of its fibres and the action, probably, of the cardiac ganglia are competent to make it contract, and the necessary intermittent dilatation of its cavities makes these contractions assume a certain regularity; but the quantity and density of the blood are subject to very considerable variations within the limits of health, which, without some regulating influence, would undoubtedly cause variations in the heart's action, so considerable as to be injurious. This is shown by the palpitating and irregular action of the heart when the pneumogastrics have been divided. These nerves convey to the heart a constant influence, which may be compared to the insensible tonicity imparted to voluntary muscles by the general motor system. When a set of muscles on one side is paralyzed, as in facial palsy, their tonicity is lost, they become flaccid, and the muscles on the other side, without any effort of the will, distort the features. An exaggeration of this force may be imitated by a feeble Faradic current, which renders the pulsations of the heart less frequent and more powerful, or it may be still farther exaggerated by a more powerful current, which arrests the action of the heart. Phemonena are not wanting in the human subject to verify these views. Causes which operate through the nervous system frequently produce palpitation and irregular action of the heart. Cases are not uncommon in which palpitation habitually occurs after a full meal. There are instances on record of death from arrest of the heart's action as a consequence of fright, anger, grief or other severe mental emotions. Syncope from these causes is by no means uncommon. In the latter instance, when the heart resumes its contractions, the nervous shock carried along the pneumogastrics is only sufficient to arrest its action temporarily. When death takes place, the shock is so great that the heart never recovers from its effects.

## Summary of Certain Causes of Arrest of the Action of the Heart.

In warm-blooded animals, the heart's action speedily ceases after the organ is deprived of its natural stimulus, the blood. Proof of this is not derived alone from experiments on the inferior animals. It is well known that in profuse hæmorrhage in the human subject, the contractions of the heart are progressively enfeebled, and when the loss of blood has proceeded to a certain extent, are permanently arrested. Cases of transfusion after hæmorrhage show that when blood is introduced the heart may be made to resume its pulsations. The same result takes place in death by asthenia; and cases are on record in which life has been prolonged, as in hæmorrhage, by transfusion of even a small quantity of healthy blood. These facts have been demonstrated on the inferior animals by experiments already cited. The experiment of Haller, in which the action of the right side of the heart of a cat was arrested by emptying it of blood, while the left side, which was filled with blood, continued to pulsate, showed that the absence of blood is competent of itself to arrest contractions of the heart. The experiments of Erichsen, who paralyzed the heart by tying the coronary arteries, and of Schiff, who produced a local paralysis by tying the vessel going to the right ventricle, show that the action of the heart may also be arrested by cutting off the circulation of blood in its substance. Both of these causes must operate in arrest of the heart's action in hæmorrhage.

The mechanical causes of arrest of the heart's action are of considerable pathological importance. The heart, in common with other muscles, may be paralyzed by mechanical injury. A violent blow upon the deltoid paralyzes the arm; a severe strain will paralyze the muscles of an extremity; and in the same way, excessive distention of the cavities of the heart will arrest its pulsations. This is shown by arrest of the circulation in asphyxia; which is due to the fact that the heart is incapable of forcing the unaërated blood through the systemic capillaries. The heart, in asphyxia, finally becomes enormously strained and distended and is consequently paralyzed. The same result follows the application of a ligature to the aorta. This effect may be produced also, in the cold-blooded animals, in which, if the heart be left undisturbed, the pulsations will continue for a long time. The following experiment illustrating this point was performed upon the heart of a large alligator :

The animal was poisoned with curare, and twenty-eight hours after death the heart, which had been exposed and left *in situ*, was pulsating regularly. It was then removed from the body, and after some experiments on the comparative force, etc., of the pulsations when empty and when filled with blood, was filled with water, the valves having been destroyed so as to allow free passage of the fluid through the cavities, and the vessels were tied. The ventricles, still filled with water confined in their cavity, were then firmly compressed with the hand. From that time, the heart entirely ceased its contractions and became hard like a muscle in a state of cadaveric rigidity.

This experiment shows how completely and promptly the heart, even of a cold-blooded animal, may be arrested in its action by mechanical injury (Flint, 1861).

Cases of death from engorgement of the heart are not unusual in practice; and the form of organic disease which most frequently leads to sudden death is that in which the heart is liable to great distention. In other lesions there is not this tendency; but when the aortic orifice is contracted or the valves are insufficient, any great disturbance of the circulation will cause the heart to become engorged, which is liable to produce a fatal result.

Most persons are practically familiar with the distressing sense of suffocation which frequently follows a blow upon the epigastrium; and a few cases are on record of instantaneous death following a comparatively slight concussion in this region. Although these cases are rare, they are well recognized, and the effects are generally attributed to injury of the solar plexus. The distress is precisely what would occur from sudden arrest of the heart's action. It is the blood charged with oxygen which supplies the wants of the tissues, and not the simple entrance of air into the lungs; and arrest of the circulation of arterial blood, from any cause, produces suffocation as completely as though the trachea were tied. It is a question whether the arrest of the heart, if this be the pathological condition, be due to concussion of the nervous centre or to the direct effects of the blow upon the organ itself. Present data do not afford a definite answer to this question, but they sustain, to a certain extent, the opinion that in such accidents, the symptoms are due to direct injury of the heart. An additional argument in favor of this view is founded on what is known of the mode of operation of the sympathetic system. The effects of stimulation or irritation of this system are not instantaneously manifested, as is the case in the cerebro-spinal system, but are developed slowly and gradually.

As far as the results of experiments are concerned, the nervous influences which arrest the action of the heart seem to operate through the pneumogastrics and are derived from the spinal accessory nerves. This action can be closely imitated by electricity. The causes of arrest in this way are many and varied. Among them may be mentioned, sudden and severe bodily pain and severe mental emotions. With the exception of arrest of the heart's action from loss of blood and from distention, from whatever cause it may occur, stoppage of the heart takes place from influences operating through the nervous system. It may be temporary, as in syncope, or it may be permanent; and examples of the latter, though rare, are sufficiently well authenticated.

In an animal just killed, as the pulsations of the heart become slower and slower until they are finally arrested, it is constantly observed that the auricular appendage on the right side continues to contract for some time after the other portions of the heart have ceased their action.

## CHAPTER III.

### *CIRCULATION OF THE BLOOD IN THE VESSELS.*

**Physiological anatomy of the arteries—Course of blood in the arteries—Locomotion of the arteries and production of the pulse—Pressure of blood in the arteries—Pressure in different parts of the arterial system—Depressor nerve—Influence of respiration on the arterial pressure—Rapidity of the current of blood in the arteries—Rapidity in different parts of the arterial system—Circulation of the blood in the capillaries—Physiological anatomy of the capillaries—Pressure of blood in the capillaries—Relations of the capillary circulation to respiration—Causes of the capillary circulation—Influence of temperature on the capillary circulation—Influence of direct irritation on the capillary circulation—Circulation of the blood in the veins—Physiological anatomy of the veins—Course of the blood in the veins—Pressure of blood in the veins—Rapidity of the venous circulation—Causes of the venous circulation—Air in the veins—Uses of the valves—Conditions which impede the venous circulation—Regurgitant venous pulse—Circulation in the cranial cavity—Circulation in erectile tissues—Derivative circulation—Pulmonary circulation—Circulation in the walls of the heart—Passage of the blood-corpuscles through the walls of the vessels (diapedesis)—Rapidity of the circulation—Phenomena in the circulatory system after death.**

In man and in all animals possessed of a double heart, each cardiac contraction forces a charge of blood from the right ventricle into the pulmonary artery, and from the left ventricle into the aorta; and the valves which guard the orifices of these vessels effectually prevent regurgitation during the intervals of contraction. There is, therefore, but one direction in which the blood can flow in obedience to this intermittent force; and the fact that even in the smallest arteries, there is an acceleration in the current coincident with each contraction of the heart, which disappears when the action of the heart is arrested, shows that the ventricular systole is the cause of the arterial circulation. The arteries have the important office of supplying nutritive matters to all the tissues and furnishing to the glands materials out of which the secretions are formed, and, in short, are the vessels of supply to every part of the organism. The supply of blood regulates, to a considerable extent, the processes of nutrition and has an important bearing on the general and special functions; and the various physiological processes necessarily demand considerable modifications in the quantity of arterial blood which is furnished to parts at different times. The force of the heart, however, varies but little within the limits of health; and the conditions necessary to the proper distribution of blood in the economy are regulated almost exclusively by the arterial system. These vessels are endowed with elasticity, by which the circulation is considerably facilitated, and with contractility, by which the supply to any part may be modified, independently of the action of the heart. Sudden flushes or pallor of the countenance are examples of the facility with which this may be effected. It is evident, therefore, that the properties of the coats of the arteries are of great physiological importance.

### Physiological Anatomy of the Arteries.

The vessels which carry the venous blood to the lungs are branches of a great trunk which takes its origin from the right ventricle. They do not differ in structure from the vessels which carry the blood to the general system, except in the fact that their coats are somewhat thinner and more distensible. The aorta, branches and ramifications of which supply all parts of the body, is given off from the left ventricle. Just at its origin, behind the semilunar valves, the aorta has three sacculated pouches, called the sinuses of Valsalva. Beyond this point the vessels are cylindrical. The arteries then branch, divide and subdivide, until they are reduced to microscopic size. The branches, with the exception of the intercostal arteries, which make nearly a right angle with the thoracic aorta, are given off at an acute angle. As a rule, the arteries are nearly straight, taking the shortest course to the parts which they supply with blood; and while the branches progressively diminish in size, but few are given off between the great trunk and small vessels which empty into the capillary system. So long as a vessel gives off no branches, its caliber does not progressively diminish; as the common carotids, which are as large at their bifurcation as they are at their origin. There are one or two instances in which vessels, although giving off many branches in their course, do not diminish in size for some distance; as the aorta, which is as large at the point of division into the iliacs as it is in the chest, and the vertebral arteries, which do not diminish in caliber until they enter the foramen magnum. It has long been remarked that the combined caliber of the branches of an arterial trunk is greater than that of the main vessel; so that the arterial system, as it branches, increases in capacity. A single exception to this rule is in the instance of the common iliacs, the combined caliber of which is less than the caliber of the abdominal aorta.

The arrangement of the arteries is such that the requisite supply of blood is sent to all parts of the economy by the shortest course and with the least possible expenditure of force by the heart. Generally the vessels are so situated as not to be exposed to pressure and consequent interruption of the current of blood; but in certain situations, as about some of the joints, there is necessarily some liability to occasional compression. In certain situations, also, as in the vessels going to the brain, particularly in some of the inferior animals, it is necessary to moderate the force of the blood-current, on account of the delicate structure of the organs in which they are distributed. Here there is a provision in the shape of anastomoses, by which, on the one hand, compression of a vessel simply diverts, and does not arrest the current of blood, and on the other hand, the current is rendered more equable and the force of the heart is moderated.

The arteries are provided with fibrous sheaths, of greater or less strength, as the vessels are situated in parts more or less exposed to disturbing influences or accidents.

The arteries have three well-defined coats. As these vary very considerably in arteries of different sizes, it will be convenient, in their description, to divide the vessels into three classes:

1. The largest arteries; in which are included all that are larger than the carotids and common iliacs.

2. The arteries of medium size; that is, between the carotids and iliacs and the smallest.

3. The smallest arteries; or those less than $\frac{1}{15}$ to $\frac{1}{12}$ of an inch (1·7 to 2·1 mm.) in diameter.

The largest arteries are very strong and elastic. Their external coat is composed of ordinary fibrous tissue, with a few longitudinal and oblique fasciculi of non-striated muscular fibres. This coat is no thicker in the largest vessels than in some of the vessels of medium size; and in some medium-sized vessels it is actually thicker than in the aorta. This is the only coat that is vascular.

The middle coat, on which the thickness of the walls of the vessel depends, is composed chiefly of yellow elastic tissue. This tissue is disposed in a number of layers. Externally there is a thin layer of ramifying elastic fibres, and then a number of layers of elastic membrane, with oval, longitudinal openings, an arrangement which has given it the name of the "fenestrated membrane." Between the different layers of this membrane are found a few non-striated muscular fibres. These muscular fibres, however, are not abundant and have but little physiological importance. A small portion of the aorta and pulmonary artery near the heart is entirely free from muscular fibres. In the largest arteries the fibres are arranged in fasciculi, with amorphous and fibrous connective tissue running in circular, longitudinal and oblique directions. The longitudinal and oblique fibres exist chiefly in the outer coat.

The internal coat of the largest arteries does not differ materially from the lining membrane of the rest of the arterial system. It is nearly identical in structure with the endocardium and is continued throughout the vascular system. It is a thin, homogeneous, elastic membrane, covered with a layer of elongated cells of endothelium, with oval nuclei, the long diameter of the cells and nuclei following the direction of the vessel. Between the endothelial cells, is an amorphous cement-substance, which is rendered dark by a solution of silver nitrate, so that this reagent clearly defines their borders.

The arteries of medium size possess considerable strength, some elasticity and very great contractility. In the outer and inner coats there is no great difference between these and the largest arteries, even in thickness. The essential difference in the anatomy of these vessels is found in the middle coat. Here there is a continuation of the elastic elements found in the largest vessels, but relatively diminished in thickness and mingled with the fusiform, non-striated muscular fibres arranged nearly always at right angles to the course of the vessel. These fibres are found chiefly in the inner layers of the middle coat and only in arteries smaller than the carotids and primitive iliacs. In arteries of medium size, like the femoral, profunda femoris, radial or ulnar, the muscular fibres exist in several layers. There is no distinct division, as regards the middle coat, between the largest arteries and those of medium size. As the arteries branch, muscular fibres make their appearance between the elastic layers, progressively increasing in quantity, while the elastic elements are diminished in their relative proportion.

In the smallest arteries, the external coat is thin and disappears just before the vessels empty into the capillary system; so that the very smallest arterioles have only the inner coat and a layer of muscular fibres. Although most of the muscular fibres in the middle coat of the arteries are arranged at right angles to the course of the vessels, nearly all of the arteries in the human subject are provided with longitudinal and oblique muscular fasciculi,

FIG. 23.—*Small artery from the mesentery of the frog, showing endothelium and circular muscular fibres; magnified 500 diameters* (from a photograph taken at the United States Army Medical Museum).

which are sometimes external, sometimes internal and sometimes on both sides of the circular layers.

The middle coat is composed of circular muscular fibres, without any admixture of elastic elements. In vessels $\frac{1}{100}$ of an inch (254 $\mu$) in diameter, there are two or three layers of fibres; but nearer the capillaries and as the vessels lose the external fibrous coat, these fibres exist in a single layer.

The internal coat presents no essential difference from the coat in other vessels, with the exception that the endothelium is rather less distinctly marked.

A tolerably rich plexus of vessels is found in the external coat of the arteries. These are called vasa vasorum and come from the adjacent arterioles, generally having no direct connection with the vessel on which they are distributed. A few vessels penetrate the external layers of the middle coat, but none are ever found in the internal coat.

Nervous filaments accompany the arteries, in all probability, to their remotest ramifications. These are not distributed in the walls of the large vessels, but follow them in their course, their filaments of distribution being found in those vessels in which the muscular element of the middle coat predominates. The vaso-motor nerves, as they are called, play an important part in regulating the processes of nutrition.

*Course of the Blood in the Arteries.*—With every pulsation of the heart, all the blood contained in the ventricles, excepting perhaps a few drops, is forced into the great vessels. The valvular arrangement by which the blood, once forced into these vessels, is prevented from returning into the ventricles during their diastole, has already been described. The foregoing sketch of the anatomy of the arteries indicates a complexity of phenomena in the circulation in these vessels, which would not obtain if they were simple, inelastic tubes. In this case, the intermittent force of the heart would be felt equally in all the vessels, and the arterial circulation would be subject to no modifications which did not come from the action of the central organ. As it is, the blood is received from the heart into vessels endowed, not only with great elasticity, but with contractility. The elasticity, which is the prominent property of the largest arteries, moderates the intermittency of the heart's action, providing a continuous supply to the parts; while the contractility of the smallest arteries is capable of increasing or diminishing the supply in any part, as may be required in the various functions.

*Elasticity of the Arteries.*—This property is particularly marked in the largest vessels. If the aorta be forcibly distended with water, it may be dilated to more than double its ordinary capacity and will resume its original size and form as soon as the pressure is removed, its elasticity being absolutely perfect. This simple experiment shows that if the force of the heart be sufficient to distend the great vessels, their elasticity during the intervals of its action must be continually forcing the blood toward the periphery. The fact that the arteries are distended at each systole has been shown by direct experiments; although the immense capacity of the arterial system, as compared with the small charge of blood which enters at each pulsation, renders the actual distention of the vessels less than would be expected from the force of the heart's contraction.

Division of an artery in a living animal illustrates one of the important phenomena due to the elastic and yielding character of its walls. It is observed, even in vessels of considerable size, as the carotid or femoral, that the flow of blood is not intermittent but remittent. With each ventricular systole there is a sudden and marked impulse; but during the intervals of contraction, the blood continues to flow with considerable force. In the smaller vessels, the impulse becomes less and less marked; but it is not entirely lost, even in the smallest vessels, the flow becoming constant only in the capillary system. That the force of the heart is absolutely intermittent, is shown by the following experiment: If the heart be exposed in a living animal, and a canula be introduced through the walls into one of the ventricles, there is a powerful jet at each systole, but no blood is discharged during the diastole. The same absolute intermittency of the current is observed in the aorta near the heart. The conversion of the intermittent current in the largest vessels into a nearly constant flow in the smallest arterioles is effected by the physical property of elasticity; and the intermittent impulse may be said to be progressively absorbed by the elastic walls of the vessels. This modification of the impulse of the heart has great physiological importance; for it is evidently essential that the current of blood, as it flows into the delicate capillary vessels, should not be alternately intermitted and impelled with the full power of the ventricle.

The elasticity of the arteries favors the flow of blood toward the capillaries by a mechanism that is easily understood. The blood discharged from the heart distends the elastic vessel, which reacts, after the distending force ceases to operate, and compresses its fluid contents. This reaction would have the effect of forcing the blood in two directions, were it not for closure of the valves, which renders regurgitation into the heart impossible. The influence, then, can be exerted only in the direction of the periphery. It is evident, therefore, that in vessels removed a sufficient distance from the heart, the force exerted on the blood by the reaction of the elastic walls is competent to produce a very considerable current during the intervals of the heart's action.

*Contractility of the Arteries.*—The medium-sized and smallest arteries contain non-striated muscular fibres; and it has been shown that as a consequence of the condition of these fibres, the vessels undergo considerable variations in their caliber. These changes in the size of the arteries can be produced by stimulation or section of the vaso-motor nerves. If the sympathetic be divided in the neck of a rabbit, the arteries of the ear on that side soon become dilated. If the divided extremity of the nerve be stimulated, the vessels contract and may become smaller than on the opposite side. These experiments demonstrate the contractile properties of the small arteries and give an idea how the supply of blood to any particular part may be regulated. The contractility of the arteries has great physiological importance. As their office is simply to supply blood to the various tissues and organs, it is evident that when the vessels going to any particular part are dilated, the supply of blood is necessarily increased. This is particularly well marked in the glands, which, during the intervals of secretion, receive a comparatively small quantity of blood. The pallor of parts exposed to cold and the flush produced by heat are due, on the one hand, to contraction, and on the other, to dilatation of the small arteries. Pallor and blushing from mental emotions are examples of the same kind of action.

The idea, which at one time obtained, that the arteries were the seat of rhythmical contractions which had a favorable influence on the current of blood is erroneous; and it is hardly necessary to repeat the statement that the cause of the arterial circulation is the force of the left ventricle. It has been observed, however, that the arteries in the ear and certain other parts in the rabbit undergo rhythmical contractions and dilatations, these occurring ten or twelve times per minute (Schiff, Lovén, Vulpian); but these movements are not to be regarded as a contributing force in the production of the circulation. It is evident, on the other hand, that the elasticity of the arteries must actually assist the circulation. The resiliency of the vessels is continually pressing their contents toward the periphery; the dilatation of the vessels with each systole of course admits an increased quantity of blood; and it has been shown that the same intermittent force exerted on an inelastic tube will discharge a less quantity of liquid from openings of equal caliber.

Superadded, then, to the direct action of the heart, physiologists now recognize, as a cause influencing the flow of blood in the arteries, the resiliency of the vessels, especially of those of large size, this force being derived originally from the heart. Thus it will be seen that the arteries are constantly kept distended with blood by the heart; and by virtue of their elasticity and the progressive increase in the capacity of this system as they branch, the powerful contractions of the central organ serve only to keep up an equable current in the capillaries. The small vessels, by the action of their contractile walls, regulate the local circulations.

*Locomotion of the Arteries and Production of the Pulse.*—With each contraction of the heart, the arteries are increased in length and many of them undergo a considerable locomotion. This may be readily observed in vessels which are tortuous in their course, and is frequently very marked in the temporal artery in old persons. The elongation may also be observed by watching attentively the point where an artery bifurcates, as at the division of the common carotid. It is simply the mechanical effect of sudden distention, which, while it increases the caliber of the vessel, causes an elongation even more marked.

The finger placed over an exposed artery or one which lies near the surface experiences a sensation at every beat of the heart as though the vessel were striking against it. This has long been observed and is called the pulse. Ordinarily it is appreciated when the current of blood is subjected to a certain degree of obstruction, as in the radial, which can readily be compressed against the bone. In an artery imbedded in soft parts which yield to pressure, the actual dilatation of the vessel being very slight, pulsation is felt with difficulty, if at all. When obstruction of an artery is complete, as after tying a vessel, the pulsation above the point of ligature is very marked and can be readily appreciated by the eye. The explanation of this exaggeration of the movement is the following: Normally, the blood passes freely through the arteries and produces, in the smaller vessels, very little movement or dilatation; when, however, the current is obstructed, as by ligation or even compression with the finger, the force of the heart is not sent through the vessel to the periphery but is arrested and therefore becomes more marked and easily appreciated. In vessels which have become undilatable and incompressible from calcareous deposits, the pulse can not be felt. The character of the pulse indicates, to a certain extent, the condition of the heart and vessels.

Under ordinary conditions, the pulse may be felt in all arteries that are exposed to investigation; and as it is due to the movement of the blood in the vessels, the prime cause of its production is the contraction of the left ventricle. The impulse given to the blood by the heart, however, is not felt in all the vessels at the same instant. Marey registered simultaneously the impulse of the heart, the pulse of the aorta and the pulse of the femoral artery, and ascertained that the contraction of the ventricle is anterior, in point of time, to the pulsation of the aorta, and that the pulsation of the aorta precedes the pulse in the femoral. This only confirmed the views of other physiologists, particularly Weber, who described this progressive retardation of the pulse, estimating the difference between the ventricular systole and the pulsation of the artery in the foot at one-seventh of a second.

It is evident from what is known of the variations which occur in the force of the heart's action, the quantity of blood in the vessels, and from the changes which may take place in the caliber of the arteries, that the characters of the pulse must be subject to great variations. Many of these may be appreciated simply by the sense of touch. Writers treat of the soft and compressible pulse, the hard pulse, the wiry pulse, the thready pulse etc., as indicating various conditions of the circulatory system. The character of the pulse, aside from its frequency, has always been regarded as of great importance in disease.

*Form of the Pulse.*—It is evident that few of the characters of a pulsation, occupying as it does but one-seventieth part of a minute, can be ascertained by the sense of touch alone. This fact has been appreciated by physiologists, and within the last few years, instruments for registering the pulse have been constructed, with the view of analyzing the dilatation and movements of the vessels. The idea of such an instrument was probably suggested by the following simple observation: When the legs are crossed,


FIG. 24.—*Sphygmograph of Marey.*

The apparatus is securely fixed on the forearm, so that the spring under the screw V is directly over the radial artery. The movements of the pulse are transmitted to the long and light wooden lever L and registered upon the surface P, which is moved at a known rate by the clock-work H. The apparatus is so adjusted that the movements of the vessel are accurately amplified and registered by the extreme point of the lever.

with one knee over the other, the beating of the popliteal artery will produce marked movements of the foot. If a lever provided with a marking-point in contact with a slip of paper moving at a definite rate could be applied to an artery, the point of the lever would register the movements of the vessel and its changes in caliber. The first physiologist who put this in practice was Vierordt, who constructed quite a complex instrument, so

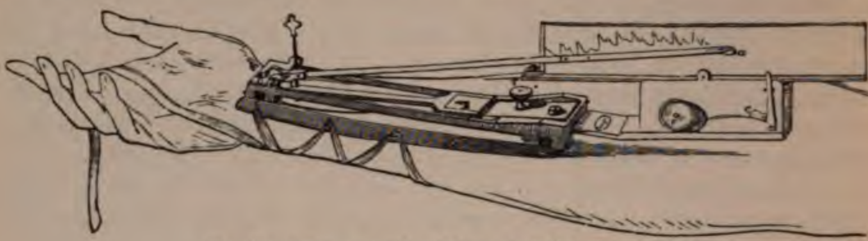

FIG. 25.—*Sphygmograph of Marey applied to the arm.*

arranged that the impulse from an accessible artery, like the radial, was conveyed to a lever, which marked the movement upon a revolving cylinder of paper. This instrument was called a sphygmograph. The traces made by it were perfectly regular and simply marked the extremes of dilatation — exaggerated, of course, by the length of the lever—and the number of pulsations in a given time. The latter can be easily estimated by more simple means; and as the former did not convey any very definite physiological idea, the apparatus was regarded rather as a curiosity than an instrument for accurate research.

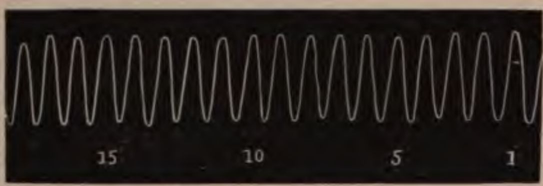


FIG. 26.—*Trace of Vierordt.*

The principle on which the instrument of Vierordt was constructed was correct; and it remained only to devise one which would be easy of application and produce a trace representing the shades of dilatation and contraction of the vessels, in order to lead to important practical results. These conditions are realized in the sphygmographs now in use, which differ from each other mainly in the convenience with which they are applied, the principle of all being substantially that of the sphygmograph of Marey, which is shown in Figs. 24 and 25. The modern sphygmographs simply amplify the changes in the caliber of the artery incident to the pulse; and although their application is, perhaps, not so easy as to make these instruments generally useful in the practice of medicine, in the hands of Marey and other physiologists, they have led to a definite knowledge of the physiological characters of the pulse and its modifications in certain diseases, information which could hardly be arrived at by other means of investigation.

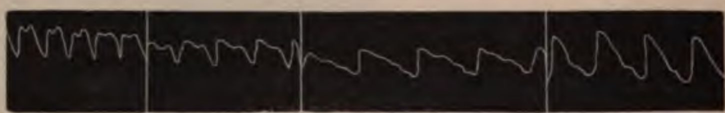

FIG. 27.—*Trace of Marey.*
Portions of four traces taken in different conditions of the pulse.

In short, their mechanism is so accurate, that when skillfully used, they give on paper the actual "form of the pulse." The modern instruments, applied to the radial artery, give traces very different from those obtained by Vierordt, which were simply series of regular elevations and depressions. A comparison of these with the traces obtained by Vierordt gives an idea of the defects which have been remedied by Marey; for it is evident that the dilatation and contraction of the arteries can not be so regular and simple as would be inferred merely from the trace made by the instrument of Vierordt.

Analyzing the traces taken by Marey, it is seen that there is a dilatation following the systole of the heart, marked by an elevation of the lever, more or less sudden, as indicated by the angle of the trace, and of greater or less amplitude. The dilatation having arrived at its maximum, is followed by reaction, which may be slow and regular, or may be, and generally is, interrupted by a second and slighter upward movement of the lever. This second impulse varies very much in amplitude. In some rare instances, it is nearly as marked as the first and may be appreciated by the finger, giving the sensation of a double pulse following each contraction of the heart. This is called the dicrotic pulse. As a rule, the first dilatation of the vessel is sudden and is indicated by an almost vertical line. This is followed by a comparatively slow reaction, indicated by a gradual descent of the trace, which is not, however, absolutely regular, but is marked by a slight elevation indicating a second impulse. The amplitude of the trace, or the distance between the highest and the lowest points marked by the lever, depends upon the degree of constant tension of the vessels. Marey has found that the amplitude is in an inverse ratio to the tension; which is very easily understood, for when the arteries are but little distended, the force of the heart must be more marked in its effects than when the pressure of blood is very great. Any condition which facilitates the flow of blood from the arteries into the capillaries will, of course, relieve the tension of the arterial system, lessen the obstacle to the force of the heart, and increase the amplitude of the pulsation, and *vice versâ*. In support of this view, Marey has found that cold applied to the surface of the body, contracting, as it does, the smallest arteries, increases the arterial tension and diminishes the amplitude of the pulsation, while a moderate elevation of temperature produces an opposite effect.

In nearly all the traces given by Marey, the descent of the lever indicates more or less oscillation of the mass of blood. The physical properties of the larger arteries render this inevitable. As they yield to the distending influence of the heart, reaction occurs after this force is taken off, and if the distention be very great, gives a second impulse to the blood. This is quite marked, unless the tension of the arterial system be so great as to offer too much resistance. One of the most favorable conditions for the manifestation of dicrotism is diminished tension, which is always found coexisting with a very marked exhibition of this phenomenon.

Marey accurately determined and registered these various phenomena, by observations on the arteries of the human subject and the lower animals; and by means of a "*schema*," representing the arterial system by elastic tubes and the left ventricle by an elastic bag provided with valves and acting as a syringe, he established the conditions of tension etc., necessary to their production. In this *schema*, the registering apparatus, simpler in construction than the sphygmograph, could be applied to the tubes with more accuracy and ease. He demonstrated by experiments with this system of tubes, that the amplitude of the pulsations, the force of the central organ being the same, is greatest when the tubes are moderately distended, or when the tension of fluid is low, and *vice versâ*. He demonstrated, also, that a low tension favors dicrotism. In this latter observation, he diminished the tension by enlarging the orifices by which the fluid was discharged from the tubes, imitating the dilatation of the small vessels, by which the tension is diminished in the arterial system. He also demonstrated that an important and essential element in the production of dicrotism is the tendency to oscillation of the fluid in the vessels during the intervals between the contractions of the heart. This can only occur in a fluid which has a certain weight and acquires a velocity from the impulse; for when air was introduced into the apparatus, dicrotism could not be produced under any conditions, as the fluid did not possess weight enough to oscillate between the impulses. Water produced a well marked dicrotic impulse under favorable conditions; and with mercury, the oscillations made two, three or more distinct impulses. By these experiments, he proved that the blood oscillates in the vessels, if this movement be not suppressed by too great pressure or tension. This oscillation gives the successive rebounds that are marked in the descending line of the pulse, and is capable, in some rare instances when the arterial tension is very slight, of producing a second rebound of sufficient force to be appreciated by the finger.

Without treating of the variations in the character of the pulse in disease, due to the action of the muscular coat of the arteries, it will be useful to consider some of the external modifying influences which come within the range of physiology. The smallest vessels and those of medium size possess to an eminent degree what is called tonicity, or the property of maintaining a certain continued degree of contraction. This contraction is antagonistic to the distending force of the blood, as is shown by opening a portion of an artery included between two ligatures in a living animal, when the contents will be forcibly discharged and the caliber of that portion of the vessel be very much diminished. Too great distention of the vessels by the pressure of blood seems to be prevented by this constant action of the muscular coat; and thus the conditions are maintained which give to the pulse the characters just described.

By excessive and continued heat, the muscular tissue of the arteries may be dilated so as to offer less resistance to the distending force of the heart. Under these conditions, the pulse, as felt by the finger, will be found to be larger and softer than normal. Cold, either general or local, has an opposite effect; the arteries become contracted, and the pulse assumes a harder and more wiry character. As a rule, prolonged contraction of the arteries is followed by relaxation, as is seen in the full pulse and glow of the surface which accompany reaction after exposure to cold. It has been found, also, that there is a considerable difference in the caliber of the arteries at different periods of the day. The diameter of the radial has been found very much greater in the evening than in the morning, producing, naturally, a variation in the character of the pulse.

### Pressure of Blood in the Arteries.

The reaction of the elastic walls of the arteries during the intervals of the heart's action gives rise to a certain degree of pressure, by which the blood is continually forced toward the capillaries. The discharge of blood into the capillaries has a constant tendency to diminish this pressure; but the contractions of the left ventricle, by forcing repeated charges of blood into the arteries, have a compensating action. By the equilibrium between these two agencies, a certain tension is maintained in the arteries, which is called the arterial pressure.

The first experiments with regard to the extent of the arterial pressure were made by Hales, an English physiologist, more than a hundred years ago. This observer, adapting a long glass tube to the artery of a living animal, ascertained the height of the column of blood which could be sustained by the arterial pressure. In some experiments on the carotid of the horse, the blood mounted to the height of eight to ten feet (243 to 304 centimetres).

If a large artery, like the carotid, be exposed in a living animal, and a metallic point, connected with a vertical tube of smaller caliber and seven or eight feet (213 or 243 centimetres) long by a bit of elastic tubing, be secured in the vessel, the blood will rise to the height of about six feet (183 centimetres) and remain at this point almost stationary, indicating, by a slight pulsatile movement, the action of the heart. On carefully watching the level in the tube, in addition to the rapid oscillation coincident with the pulse, another oscillation will be observed, which is less frequent and which corresponds with the movements of respiration. The pressure, as indicated by an elevation of the fluid, is slightly increased during expiration and diminished during inspiration. In such experiments, it is necessary to fill part of the tube, or whatever apparatus be used, with a solution of sodium carbonate, in order to prevent coagulation of the blood as it passes out of the vessels.

The experiment with the long tube gives, perhaps, the best general idea of the arterial pressure, which will be found to vary between five and a half and six feet of blood (170 and 183 centimetres), or a few inches more of water. The oscillations produced by the contractions of the heart are not very marked, on account of the great friction in so long a tube; but this is favorable to the study of the constant pressure. It has been found that the estimates above given do not vary very much in animals of different sizes. Bernard found the pressure in the carotid of a horse but little more than in the dog or rabbit. In the larger animals, it is the force of the heart which is increased, and not, to any considerable extent, the constant pressure in the vessels.

The experiments of Hales were made with a view of calculating the force of the heart, and were not directed particularly to the modifications and variations of the arterial pressure. It is only since the experiments performed by Poiseuille with the hæmadynamometer, in 1828, that physiologists have had any reliable data on this latter point. Poiseuille's instrument for measuring the force of the blood is a simple, graduated U-tube, half filled with mercury, with one arm bent at a right angle, so that it can easily be connected with the artery. The pressure of the blood is indicated by a depression in the level of the mercury on one side and a corresponding elevation on the other. This instrument is generally considered as possessing great advantages over the long glass tube; but for estimating simply the arterial pressure, it is much less useful, as it is more sensitive to the impulse of the heart. For the study of the cardiac pressure, it has the disadvantage, in the first place, of considerable friction, and again, the weight of the column of mercury produces an extent of oscillation by its mere impetus, greater than that which would actually represent the alternation of systole and diastole of the heart.

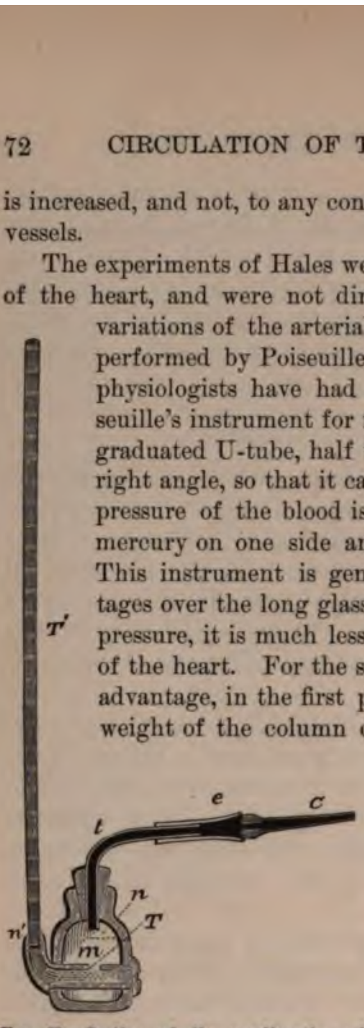


FIG. 28.—*Section of the cardiometer of Magendie, as modified by Bernard.*

A strong glass bottle is perforated at each side and fitted with an iron tube, with an opening, T, by which the mercury enters. One end of the iron tube is closed, and the other is bent upward and connected with the graudated glass tube T′, which has a caliber of $\frac{1}{12}$ to $\frac{1}{8}$ of an inch (2·1 to 3·2 mm.). The bottle is filled with mercury *m*, until it rises to *n′* in the tube, which is marked zero. The cork is perforated by the tube *t*, which is connected by a rubber tube *e* with the point C, which is introduced into the vessel.

An important improvement in the hæmadynamometer was made by Magendie. This apparatus, the cardiometer, in which Bernard made some important modifications, is the one now generally used. It consists of a small but thick glass bottle, with a fine, graduated glass tube about twelve inches (30·5 centimetres) in length, communicating with it, either through the stopper or by an orifice in the side. The stopper is pierced by a bent tube which is to be connected with the blood-vessel. The bottle is filled with mercury so that it will rise in the tube to a point which is marked zero. It is evident that the pressure on the mercury in the bottle will be indicated by an elevation in the graduated tube; and, moreover, from the fineness of the column in the tube, some of the inconveniences which are due to the weight of mercury in the hæmadynamometer are avoided, and there is, also, less friction. This instrument is appropriately called the cardiometer, as it indicates most accurately, by the extreme elevation of the mercury, the force of the heart; but it is not as perfect in its indications of the mean arterial pressure, for in the abrupt descent of the mercury during the diastole of the heart, the impetus causes the level to fall below the real standard of the constant pressure. Marey has corrected this difficulty in the "compensating" instrument, which is constructed on the following principle: Instead of a simple glass tube which communicates with the mercury in the bottle, as in Magendie's cardiometer, there are two tubes, one of which is like the one already described and represents oscillations produced by the heart, while the other is larger, and has, at the lower part, a constriction of its caliber, which is here reduced to capillary fineness. The latter tube is designed to give the mean arterial pressure; the constricted portion offering such an obstacle to the rise of the mercury that the intermittent action of the heart is not felt, the mercury rising slowly to a certain level, which is constant and varies only with the constant pressure in the vessels.

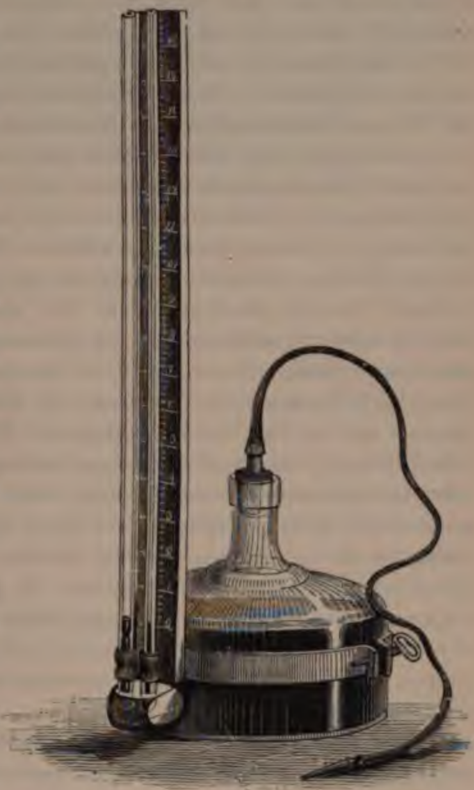

FIG. 29.—*Compensating instrument of Marey.*

Physiologists have only an approximative idea of the arterial pressure in the human subject, derived from experiments on the inferior animals. It has already been stated to be equal to about six feet (183 centimetres) of water or six inches (150 mm.) of mercury.

*Pressure in Different Arteries.*—The experiments of Hales, Poiseuille, Bernard and others, seem to show that the constant arterial pressure does not vary much in arteries of different sizes. These physiologists experimented particularly on the carotid and crural, and found the pressure in these two vessels about the same. From their experiments they concluded that the force is equal in all parts of the arterial system. The experiments of Volkmann, however, have shown that this conclusion is not correct. With the registering apparatus of Ludwig, he took the pressure in the carotid and the metatarsal arteries and always found a considerable difference in favor of the former. In an experiment on a dog, he found the pressure equal to about seven inches (172 mm.) in the carotid, and 6·6 inches (165 mm.) in the metatarsal. In an experiment on a calf, the pressure was 4·64 inches (116 mm.) in the carotid, and 3·56 inches (89 mm.) in the metatarsal; and in a rabbit, 3·64 inches (91 mm.) in the carotid, and 3·44 inches (86 mm.) in the crural. These experiments show that the pressure is not absolutely the same in all parts of the arterial system, that it is greatest in the arteries nearest the heart, and that it gradually diminishes toward the capillaries. The difference is very slight, almost inappreciable, except in vessels of very small size; but here the pressure is directly influenced by the discharge of blood into the capillaries. The cause of this diminution of pressure in the smallest vessels is the proximity of the great outlet of the arteries, the capillary system; for, as will be seen farther on, the flow into the capillaries has a constant tendency to diminish the pressure in the arteries.

*Influence of Respiration.*—It is easy to see in studying the arterial pressure, that there is a marked increase with expiration and a diminution with inspiration. In tranquil respiration the influence upon the flow of blood is due simply to the mechanical action of the thorax. With every inspiration the air-cells are enlarged, as well as the blood-vessels of the lungs, the air rushes in through the trachea, and the movement of the blood in the veins near the chest is accelerated. At the same time the blood in the arteries is somewhat retarded in its flow from the thorax, or at least does not feel the expulsive influence which follows with the act of expiration. The arterial pressure at that time is at its minimum. With the expiratory act the air is expelled by compression of the lungs, the flow of blood into the thorax by the veins is retarded to a certain extent, while the flow of blood into the arteries is favored. This is strikingly exhibited in the augmented force, with expiration, in the jet from a divided artery. Under these conditions the arterial pressure is at its maximum. In perfectly tranquil respiration, the changes due to inspiration and expiration are slight, presenting a difference of not more than half an inch or an inch (12·7 or 25·4 mm.) in the cardiometer. When the respiratory movements are exaggerated, the oscillations are very much more marked.

Interruption of respiration is followed by a very great increase in the arterial pressure. This is due, not to causes within the chest, but to obstruction to the circulation in the capillaries. With an interruption of the respiratory movements, the non-aërated blood passes into the arteries but can not flow readily through the capillaries, and as a consequence, the arteries are abnormally distended and the pressure is greatly increased. If respiration be permanently arrested, the arterial pressure becomes, after a time, diminished below the normal standard, and is finally abolished on account of the stoppage of the action of the heart. If respiration be resumed before the action of the heart has become arrested, the pressure soon returns to its normal standard.

*Influence of Muscular Action etc.*—Muscular effort considerably increases the arterial pressure. This is due to two causes. In the first place, the chest is generally compressed, and this favors the flow of blood into the great vessels. In the second place, muscular exertion produces a certain degree of obstruction to the discharge of blood from the arteries into the capillaries. Experiments upon the inferior animals show a great increase in pressure in the struggles which occur during severe operations. It has been shown that stimulation of the sympathetic in the neck and of certain of the cerebro-spinal nerves increases the arterial pressure, probably from an influence on the muscular coats of some of the arteries, causing them to contract and thereby diminishing the total capacity of the arterial system.

*Effects of Hæmorrhage etc.*—Diminution in the quantity of blood has a remarkable effect upon the arterial pressure. If, in connecting the instrument with the arteries, even one or two jets of blood be allowed to escape, the pressure will be found diminished perhaps one-half or even more. It is hardly necessary to discuss the mechanism of the effect of the loss of blood on the tension of the vessels, but it is remarkable how soon the pressure in the arteries regains its normal standard after it has been lowered by hæmorrhage. As the pressure depends largely upon the quantity of blood, as soon as the vessels absorb the serosities in sufficient quantity to repair the loss, the pressure is increased. This takes place in a very short time, if the loss of blood be not too great.

Experiments on the arterial pressure, with the cardiometer, have verified the fact stated in treating of the form of the pulse; namely, that the pressure in the vessels bears an inverse ratio to the distention produced by the contractions of the heart. In the cardiometer, the mean height of the mercury indicates the constant, or arterial pressure; and the oscillations, the distention produced by the heart. It is found that when the pressure is great, the extent of oscillation is small, and *vice versâ*. It will be remembered that the researches of Marey demonstrated that an increase of the arterial pressure diminishes the amplitude of the pulsations, as indicated by the sphygmograph, and that the amplitude is very great when the pressure is slight. It is also true, as a general rule, that the force of the heart, as indicated by the cardiometer, bears an inverse ratio to the frequency of its pulsations.

*Depressor Nerve of the Circulation.*—Cyon and Ludwig have described a nerve arising in the rabbit, by two roots, one from the main trunk of the pneumogastric and the other from the superior laryngeal nerve, which joins the sympathetic filaments in the chest and passes to the heart. In man the depressor nerve is not isolated, but its fibres are contained in the sheath of the pneumogastric. This nerve has a reflex action, as was shown by the experiments of Cyon, its Faradization reducing the arterial pressure by one-third or one-half. This action is known to be reflex, for when the nerve is divided, stimulation of the central end affects the arterial pressure, while no such result follows stimulation of the peripheral extremity; and the effect is manifested when the pneumogastrics have been divided and no direct nervous influence is exerted over the heart. It is thought that the reduction in the arterial pressure following stimulation of the so-called depressor nerves is due mainly to the action of the splanchnic nerves, by which the abdominal vessels become largely dilated. If the abdomen be opened and one or more of the splanchnic nerves be divided, the arterial pressure is immediately diminished, and the pressure is restored if the divided ends of the nerves be stimulated. If, after division of the splanchnic nerves and the consequent diminution of the arterial pressure, the depressor nerves be stimulated, the pressure still undergoes some additional diminution, but this is much less than the diminution which follows stimulation of the depressor nerves with-without section of the splanchnics.

*Rapidity of the Current of Blood in the Arteries.*—The question of the rapidity of the arterial circulation has long engaged the attention of physiologists; but the experiments of Volkmann, with his hæmadrometer, and of Vierordt, with a peculiar instrument which he devised for the purpose, did not lead to results that were entirely reliable. The apparatus devised by Chauveau, however, is much more satisfactory. This will give, by calculation, the actual rapidity of the circulation, and it also indicates the variations in velocity which occur at different periods of the heart's action.

The instrument to be applied to the carotid of the horse consists of a thin brass tube, about an inch and a half (38·1 mm.) in length and of the diameter of the artery (about three-eighths of an inch, or 9·5 mm.), which is provided with an oblong, longitudinal opening, or window, near the middle, about two lines (4·2 mm.) long and one line (2·1 mm.) wide. A piece of thin, vulcanized rubber is wound around the tube and firmly tied so as to cover this opening. Through a transverse slit in the rubber, is introduced a very light, metallic needle, an inch and a half (38·1 mm.) in length and flattened at its lower part. This is made to project about half-way into the caliber of the tube. A flat, semicircular piece of metal, divided into an arbitrary scale, is attached to the tube, to indicate the deviations of the point of the needle.

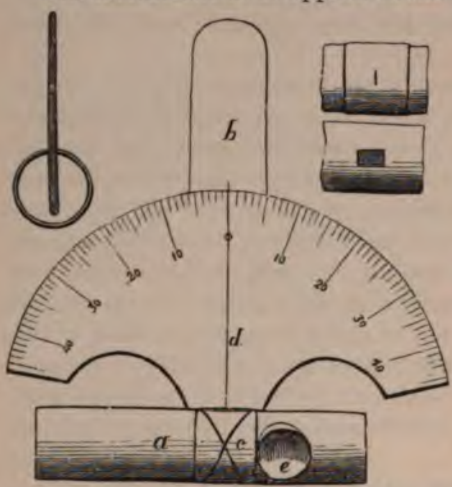


FIG. 30.—*Chauveau's instrument for measuring the rapidity of the flow of blood in the arteries.*

The instrument viewed in face—*a*, the tube to be fixed in the vessel; *b*, the dial which marks the extent of movement of the needle *d*; *e*, a lateral tube for the attachment of a cardiometer, if desired.

The apparatus is introduced into the carotid of a horse, by making a slit in the vessel, introducing first one end of the tube directed toward the heart, then allowing a little blood to enter the instrument, so as to expel the air, and, when full, introducing the other end, securing the whole by ligatures above and below.

When the circulation is arrested, the needle should be vertical, or mark zero on the scale. When the flow is established, a deviation of the needle occurs, which varies in extent with the rapidity of the current. Having removed all pressure from the vessel so as to allow the current to resume its normal character, the deviations of the needle are carefully noted, as they occur with the systole of the heart, with the diastole etc. After withdrawing the instrument, it is applied to a tube of the size of the artery, in which a current ot water is made to pass with a rapidity which will produce the same deviations as occurred when the instrument was connected with the blood-vessel. The rapidity of the current in this tube may be easily calculated by receiving the fluid in a graduated vessel and noting the time occupied in discharging a given quantity. By this means the rapidity of the current of blood is ascertained. This instrument is made on the same principle as the one constructed by Vierordt, but in sensitiveness and accuracy it is much superior.

*Rapidity of the Current in the Carotid.*—It has been found that three currents, with different degrees of rapidity, may be distinguished in the carotid:

1. At each ventricular systole, as the average of the experiments of Chauveau, the blood moves in the carotids at the rate of about 20·4 inches (510 mm.) per second. After this, the rapidity quickly diminishes and the needle returns quite or nearly to zero, which would indicate complete arrest.

2. Immediately succeeding the ventricular systole, a second impulse is given to the blood, which is synchronous with the closure of the semilunar valves, the blood moving at the rate of about 8·6 inches (215 mm.) per second. This is the dicrotic impulse.

3. After the dicrotic impulse, the rapidity of the current gradually diminishes until just before the systole of the heart, when the needle is nearly at zero. The average rate, after the dicrotic impulse, is about 5·9 inches (147·5 mm.) per second.

The experiments of Chauveau correspond with the experiments of Marey on the form of the pulse. Marey showed that there is a marked oscillation of the blood in the vessels, due to a reaction of their elastic walls, following the first violent distention by the heart; that at the time of closure of the semilunar valves, the arteries present a second, or dicrotic distention, much less than the first; and following this, there is a gradual decline in the distention until the minimum is reached. According to the observations of Chauveau, corresponding to the first dilatation of the vessels, the blood moves with great rapidity; following this, the current suddenly becomes nearly arrested; this is followed by a second acceleration in the current, less than the first; and following this, there is a gradual decline in the rapidity, to the time of the next pulsation.

*Rapidity in Different Parts of the Arterial System.*—From the fact that the arterial system progressively increases in capacity, there should be found a corresponding diminution in the rapidity of the flow of blood. There are, however, many conditions, aside from simple increase in the capacity of the vessels, which modify the blood-current and render inexact any calculations made upon purely physical principles. There are the tension of the blood, the conditions of contraction or relaxation of the smallest arteries, etc. It is necessary, therefore, to have recourse to actual experiments to arrive at any definite results on this point. Volkmann found a great difference in the rapidity of the current in the carotid and metatarsal arteries, the averages being about 10 inches (254 mm.) per second in the carotid, and about 2·2 inches (56 mm.) in the metatarsal. The same difference, although not quite so marked, was found by Chauveau, between the carotid and the facial. The last-named observer also noted an important modification in the character of the current in the smaller vessels. As the vessels are farther and farther removed from the heart, the systolic impulse becomes rapidly diminished, being reduced in one experiment about two-thirds; the dicrotic impulse becomes feeble or may even be abolished; but the constant flow is much increased in rapidity. This fact coincides with the ideas already advanced with regard to the gradual conversion, by reason of the elasticity of the vessels, of the impulse of the heart into first, a remittent, and in the very smallest arteries, a nearly constant current.

The rapidity of the flow in any artery must be subject to constant modifications due to the condition of the arterioles which are supplied by it. When these little vessels are dilated, the artery of course empties itself with greater facility and the rapidity is increased. Thus the rapidity bears a relation to the arterial pressure; as variations in the pressure depend chiefly on causes which facilitate or retard the flow of blood into the capillaries. A good example of enlargement of the capillaries of a particular part is in mastication, when the salivary glands are brought into activity and the quantity of blood which they receive is greatly increased. Chauveau found a great increase in the rapidity of the flow in the carotid of a horse during mastication. It must be remembered that in all parts of the arterial system, the rapidity of the current of blood is constantly liable to increase from dilatation of the small vessels and to diminution from their contraction.

## CIRCULATION OF THE BLOOD IN THE CAPILLARIES.

Before entering upon the study of the capillary circulation, it should be distinctly stated what is meant by capillary vessels as distinguished from the smallest arteries and veins. From a strictly physiological point of view, the capillaries are to be regarded as beginning at the situation where the blood is brought near enough to the tissues to enable them to separate the matters necessary for their regeneration and to give up the products of their physiological wear; but at present it is impossible to assign any limit where the vessels cease to be simple carriers of blood, and it is not known to what part of the vascular system the processes of nutrition are exclusively confined. The divisions of the blood-vessels must be, to a certain extent, arbitrarily defined. The most simple, and

FIG. 31.—*Capillary blood-vessels* (Landois).
The boundaries of the cells (cement-substance between the endothelium) is blackened with silver nitrate. The nuclei of the endothelium are brought out by staining.

what seems to be the most physiological view, is to regard as capillaries those vessels which have but a single coat; for in these, the blood is brought in closest proximity to the tissues. Vessels which are provided, in addition, with a muscular or with muscular and fibrous coats are to be regarded either as small arteries or as venous radicles. This view is favored by the character of the currents of blood as seen in microscopical observation of the circulation in transparent parts. Here an impulse is observed with each contraction of the heart, until the vessels have but one coat and are so narrow as to allow the passage of but a single line of blood-corpuscles.

*Physiological Anatomy of the Capillaries.*—If the arteries be followed out to their minutest ramifications, they will be found progressively diminishing in size as they branch, and their coats, especially the muscular coat, becoming thinner and thinner, until at last they present an internal, structureless coat lined by endothelium with oval, longitudinal nuclei, a middle coat formed of but a single layer of circular muscular fibres, and an external coat composed of a very thin layer of longitudinal bundles of fibrous tissue. These vessels are $\frac{1}{400}$ to $\frac{1}{200}$ of an inch (62·5 to 125 $\mu$) in diameter. They become smaller as they branch, and undoubtedly possess the property of contractility, which is particularly marked in the arterial system. Following the course of the vessels, when they are reduced in size to about $\frac{1}{800}$ of an inch (31 $\mu$), the external, fibrous coat is lost, and the vessel then presents only the internal coat and a single layer of muscular fibres. The vessels become smaller as they branch, finally lose the muscular fibres, and have then but a single coat. These last will be regarded as the true capillary vessels.

It was formerly thought that the smallest vessels, which are described as the true capillaries, were composed of a single, homogeneous membrane, $\frac{1}{25000}$ to $\frac{1}{2500}$ of an inch (1 to 10 $\mu$) thick, with nuclei embedded in its substance, but not provided with an endothelial lining; but it has been shown that the membrane is homogeneous, elastic, perhaps contractile, and, in some parts at least, provided with fusiform or polygonal endothelium of excessive tenuity. The borders of the endothelial cells may be seen after staining the vessels with silver nitrate. In the smallest capillaries the cells are narrow and elongated or fusiform; and in the larger vessels they are more polygonal, with very irregular borders. The nuclei in the walls of the vessels belong to this layer of endothelium. By the same process of staining with silver nitrate, irregular, non-nucleated areas are frequently brought into view; and it has been supposed by some that these indicate the presence of stomata, or orifices in the walls of the vessels.

The diameter of the capillaries is generally as small as that of the blood-corpuscles, or it may be smaller; so that these bodies always move in a single line and must become deformed in passing through the smallest vessels, recovering their normal shape, however, when they pass into vessels of larger size. The capillaries are smallest in the nervous and muscular tissue, retina and patches of Peyer, where they have a diameter of $\frac{1}{6000}$ to $\frac{1}{4000}$ of an inch (4·25 to 6·25 $\mu$). In the papillary layer of the skin and in the mucous membranes, they are $\frac{1}{4000}$ to $\frac{1}{2500}$ of an inch (6·25 to 10 $\mu$) in diameter.

They are largest in the glands and bones, where they are $\frac{1}{3000}$ to $\frac{1}{2000}$ of an inch (8·3 to 12·5 $\mu$) in diameter. These measurements indicate the size of the vessels and not their caliber. Taking out the thickness of their walls, it is only the very largest of them that will allow the passage of a blood-disk without a change in its form. The average length of the capillary vessels is about $\frac{1}{50}$ of an inch (0·5 mm.).

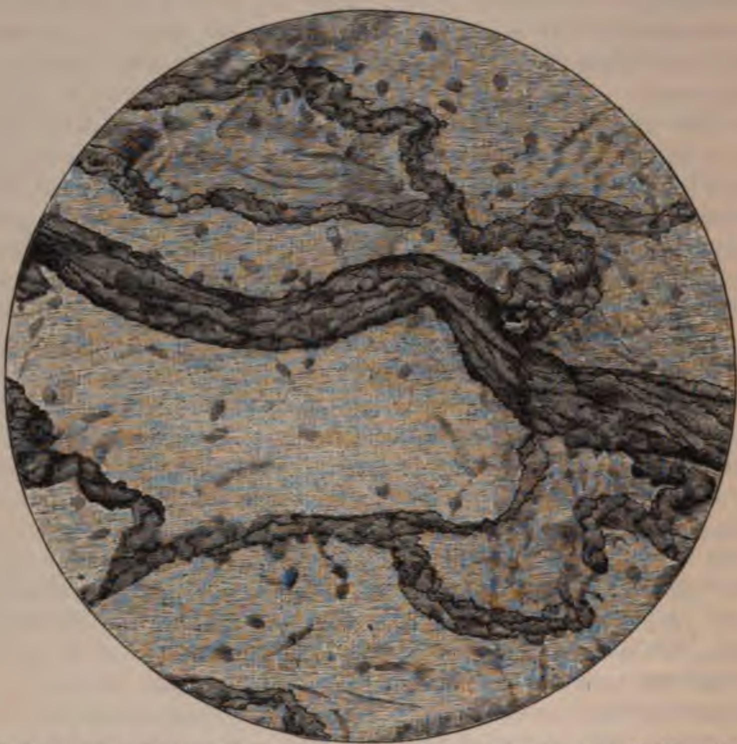

FIG. 32.—*Small artery and capillaries from the muscular coats of the urinary bladder of the frog; magnified 400 diameters* (from a photograph taken at the United States Army Medical Museum). This preparation shows the endothelium of the vessels. It is injected with silver nitrate, stained with carmine and mounted in Canada balsam.

Unlike the arteries, which grow smaller as they branch, and the veins, which become larger, in following the course of the blood, by union with each other, the capillaries form a true plexus of vessels of nearly uniform diameter, branching and inosculating in every direction and distributing blood to the parts as their physiological necessities demand. This mode of inosculation is peculiar to these vessels, and the plexus is rich in the tissues, as a general rule, in proportion to the activity of their nutrition. Although their arrangement presents certain differences in different organs, the capillary vessels have everywhere the same general characteristics, the most prominent of which are the nearly uniform diameter and an absence of any definite direction. The net-work thus formed is very rich in the substance of the glands and in the organs of absorption; but the vessels are distended with blood only during the physiological activity of these parts. In the lungs the meshes are particularly close. In other parts the vessels are not so abundant, presenting great variations in different tissues. In the muscles and nerves, in which nutrition is very active, the supply is much more abundant than in other parts, like fibro-serous membranes, tendons etc. In none of the tissues do the capillaries penetrate the anatomical elements of the part, as the ultimate muscular or nervous fibres. Some tissues receive no blood, or at least they contain no vessels which are capable of carrying red blood, and are nourished by imbibition of the nutrient plasma of the circulating fluid. Examples of these, which are called extra vascular tissues, are cartilage, nails and hair.

The capacity of the capillary system is very great. It is necessary only to consider the great vascularity of the skin, mucous membranes or muscles, to appreciate this fact. In injections of these parts, it seems, on microscopical examination, as though they contained nothing but capillaries; but in preparations of this kind, the elastic and yielding coats of the capillaries are distended to their utmost limit. Under some conditions, in health, they are largely distended with blood, as in the mucous lining of the alimentary canal during digestion, the whole surface presenting a vivid-red color, indicating the great richness of the capillary plexus. Estimates of the capacity of the capillary system, as compared with the arterial system, have been made, but they are simply approximative. The various estimates given are founded upon calculations from microscopical examinations of the rapidity of the capillary circulation as compared with the circulation in the arteries. In this way, it has been estimated that the capacity of the capillary system is between five hundred and eight hundred times that of the arterial system. These estimates, however, must be regarded as mere suppositions based upon no very accurate data.

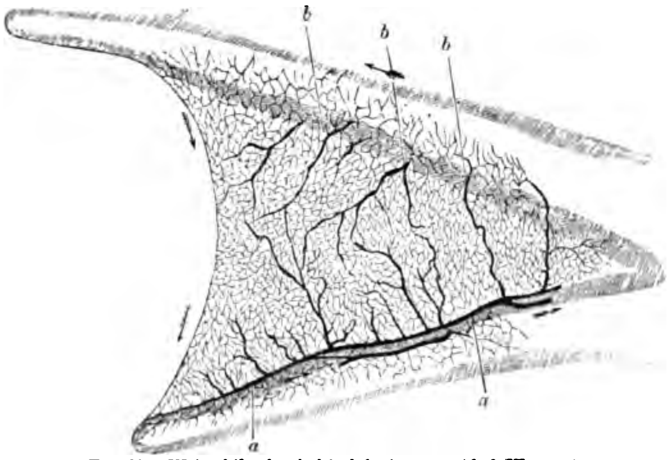

FIG. 33.—*Web of the frog's hind-foot; magnified* (Wagner). *a, a*, veins; *b, b, b*, arteries.

*Phenomena of the Capillary Circulation.*—The most convenient situation for observation of the capillary circulation is the tongue or the web of the frog. Here may be studied, not only the movement of the blood in the true capillaries, but the circulation in the smallest arteries and veins, the variations in caliber of these vessels, especially the arterioles, by the action of their muscular coat, and, indeed, the action of vessels of considerable size. This has been a valuable means of studying the circulation in the capillaries as contrasted with the flow in the small arteries and veins, and the only one, indeed, which could give any definite idea of the action of these vessels.

In studying the circulation under the microscope, the anatomical division of the blood into corpuscles and a clear plasma is observed. This is peculiarly evident in cold-blooded animals, the corpuscles being comparatively large and floating in a plasma which forms a distinct layer next the walls of the vessel. The leucocytes, which are much fewer than the red corpuscles, are generally found in the layer of plasma.


FIG. 34.—*Circulation in the web of the frog's foot* (Wagner). The black spots, some of them star-shaped, are collections of pigment. *a*, a venous trunk, composed of three principal branches (*b*, *b*, *b*), and covered with a plexus of smaller vessels (*c*, *c*).

In vessels of considerable size as well as in some capillaries, the corpuscles, occupying the central portion, move with much greater rapidity than the rest of the blood, leaving a layer of clear plasma at the sides, which is nearly motionless. This phenomenon is in obedience to a physical law regulating the passage of liquids through capillary tubes for which they have an attraction, such as exists, for example, between the blood and the vessels. In tubes reduced to a diameter approximating that of the capillaries, the attractive force exerted by their walls upon a liquid, causing it to enter the tube to a certain distance, becomes an obstacle to the passage of fluid in obedience to pressure. Of course, as the diameter of the tube is reduced, this force becomes relatively increased, for a larger proportion of the liquid contents is brought in contact with it. In the smallest arteries and veins, and still more in the capillaries, the capillary attraction is sufficient to produce the motionless layer, sometimes called the "still layer," and the liquid moves only in the central portion. The plasma occupies the position next the walls of the vessels, for it is this portion of the blood which is capable of "wetting" the tubes. The transparent layer was observed by Malpighi, Haller and all who have described the capillary circulation. Poiseuille recognized its true relation to the blood-current and explained the phenomenon of the still layer by physical laws, which had been previously established with regard to the flow of liquids in tubes of the diameter of one twenty-fifth to one one-eighth of an inch (1 to 3·2 mm.), but which he had succeeded in applying to tubes of the size of the capillaries.

A red corpuscle occasionally becomes involved in the still layer, when it moves slowly, turning over and over, or even remains stationary for a time,

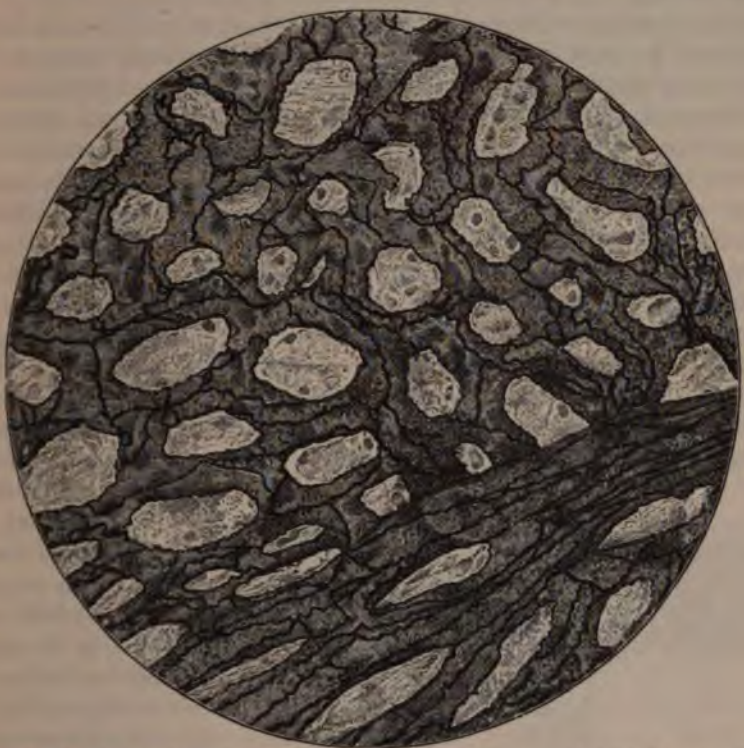

FIG. 35.—*Small artery and capillaries from the lung of a frog; magnified 500 diameters* (from a photograph taken at the United States Army Medical Museum).

until it is taken up again and carried along with the central current. A few leucocytes are constantly seen in this layer. They move along slowly and apparently have a tendency to adhere to the walls of the vessel. This is due to the adhesive character of the surface of the white corpuscles as compared with the red, which can easily be observed in examining a drop of blood between glass surfaces, the red corpuscles moving about freely, while the white corpuscles have a tendency to adhere to the glass.

Great differences exist in the character of the flow of blood in the three varieties of vessels which are under observation. In the arterioles, which may be distinguished from the capillaries by their size and the presence of the muscular and fibrous coats, the movement is distinctly remittent, even in their most minute ramifications. The blood moves in them with much greater rapidity than in either the capillaries or veins. They become smaller as they branch, and carry the blood always in the direction of the capillaries. The veins, which are relatively larger than the arteries, carry the blood more slowly and in a continuous stream from the capillaries toward the heart. In both the arteries and veins the current is frequently so rapid that the form of the corpuscles can not be distinguished. Only a few of the white corpuscles occupy the still layer, the others being carried on in the central current.

The circulation in the true capillaries is *sui generis*. Here the blood is distributed in every direction, in vessels of nearly uniform diameter. The vessels are generally so small as to admit but a single row of corpuscles. In a single vessel, a line of corpuscles may be seen moving in one direction at one moment, a few moments after, taking a directly opposite course. When the circulation is normal, the movement in the capillaries is always quite slow as compared with the movement in the arterioles, and is continuous. Here, at last, the intermittent impulse of the heart is lost. The corpuscles do not necessarily circulate in all the capillaries that are in the field of view. Certain vessels may not receive a corpuscle for some time, but afterward, one or two corpuscles become engaged in them and a current is established. A corpuscle is sometimes seen caught at the angle where a vessel divides into two, remaining fixed for a time, distorted and bent by the force of the current. It soon becomes released, and as it enters the vessel, it regains its original form. In some of the vessels of smallest size, the corpuscles are slightly deformed as they pass through. The scene is changed with every different part which is examined. In the tongue, in addition to the arterioles and venules with the rich net-work of capillaries, dark-bordered nerve-fibres, striated muscular fibres, and epithelium can be distinguished. In the lungs large, polygonal air-cells are observed, bounded by capillary vessels, in which the corpuscles move with great rapidity. It has been observed, also, that the larger vessels in the lungs are crowded to their utmost capacity with corpuscles, leaving no still layer next the walls, such as is seen in the circulation in other situations.

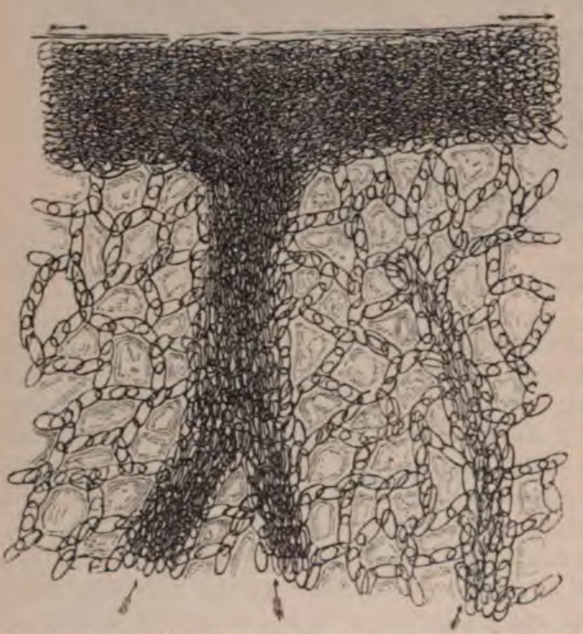

FIG. 36.—*Portion of the lung of a live triton, drawn under the microscope and magnified 150 diameters* (Wagner).

*Pressure of Blood in the Capillaries.*—There is, apparently, no way of directly estimating the pressure of blood in the capillaries. If, however, a glass plate be placed upon a part in which the capillary circulation is active and be weighted until the subjacent capillaries are emptied, an approximate idea of the blood-pressure in the vessels may be obtained. Experiments made in this way, by Von Kries, show that the pressure in the capillaries of the hand raised above the head is equal to a little less than one inch (24 mm.) of mercury; in the hand hanging down, a little more than two inches (54 mm.); and in the ear, about 0·8 of an inch (20 mm).

*Rapidity of the Capillary Circulation.*—The circulation in the capillaries of a part is subject to such great variations and the differences in different situations are so considerable, that it is impossible to give any definite rate which will represent the general rapidity of the capillary circulation. It is for this reason that it has been found impracticable to estimate accurately the capacity of the capillary as compared with the arterial system. In view of the great uncertainty in the methods employed in the estimation of the rapidity of the flow of blood in the capillaries, it seems unnecessary to discuss this question fully. Volkmann calculated the rapidity in the mesentery of the dog and found it to be about one-thirtieth of an inch (0·85 mm.) per second. Vierordt made a number of curious observations upon himself, by which he professed to be able to estimate the rapidity of the circulation in the little vessels of the eye; and by certain calculations, he formed an estimate of its rapidity, putting it at one-fortieth to one-twenty-eighth of an inch (0·63 and 0·9 mm.) per second, which estimate may be provisionally adopted as the probable rate in the human subject.

*Relations of the Capillary Circulation to Respiration.*—In treating of the influence of respiration upon the action of the heart, the arterial pressure, pulse etc., it has already been stated that non-aërated blood can not circulate freely in the capillaries. Various ideas with regard to the effects of asphyxia upon the circulation have been advanced, which will be again discussed in connection with the physiology of respiration. It is well known that arrest of respiration produces arrest of circulation.

The immediate effects of asphyxia upon the circulation are referable to the general capillary system. In a series of experiments made in 1857, the medulla oblongata was broken up, and the web of the foot was submitted to microscopical examination. This operation does not interfere with the circulation, which may be observed for hours without difficulty. The cutaneous surface was then coated with collodion, care only being taken to avoid the web under observation. The effect on the circulation was immediate. It instantly became less rapid, until, at the expiration of twenty minutes, it had entirely ceased. The entire coating of collodion was then instantly peeled off. Quite a rapid circulation immediately began, but it soon began to decline and in twenty minutes had almost ceased. In another observation, the coating of collodion was applied without destroying the medulla. The circulation was affected in the same manner as before and ceased in twenty-five minutes (Flint). These experiments, taken in connection with observations on the influence of asphyxia upon the arterial pressure, show that non-aërated blood can not circulate freely in the systemic capillaries. Non-aërated blood, however, can be forced through them with a syringe, and even in asphyxia, it passes slowly into the veins. If air be admitted to the lungs before the heart has lost its contractility, the circulation is restored. No differences in the capillary circulation have been noticed accompanying the ordinary acts of inspiration and expiration.

*Causes of the Capillary Circulation.*—The contractions of the left ventricle are evidently capable of giving an impulse to the blood in the smallest arterioles; for a marked acceleration of the current accompanying each systole can be distinguished in all but the true capillaries. It has also been shown by experiments after death, that blood can be forced through the capillary system and returned by the veins by a force less than that exerted by the left ventricle. This, however, can not rigidly be applied to the natural circulation, as the smallest arteries during life are endowed with contractility, which is capable of modifying the blood-current. Sharpey adapted a syringe, with a hæmadynamometer attached, to the aorta of a dog just killed, and found that fresh defibrinated blood could be made to pass through the double capillary systems of the intestines and liver, by a pressure of three and a half inches (89 mm.) of mercury. It spurted out at the vein in a full jet under a pressure of five inches (127 mm.). In this observation, the aorta was tied just above the renal arteries. The same pressure, the ligature being removed, forced the blood through the capillaries of the inferior extremities.

It is thus seen that the pressure in the arteries which forces the blood toward the capillaries is competent, unless opposed by contraction of the arterioles, not only to cause the blood to circulate in the capillaries, but to return it to the heart by the veins; and the only questions to be considered are first, whether there be any reason why the force of the heart should not operate on the blood in the capillaries, and second, whether there be any force in these vessels which is superadded to the action of the heart. The first of these questions is answered by microscopical observations on the circulation. A distinct impulse, following each ventricular systole, is observed in the smallest arteries; the blood flows from them directly and freely into the capillaries; and there is no ground for the supposition that the force is not propagated to this system of vessels. There is, therefore, a force, the action of the heart, which is capable of producing the capillary circulation; and there is nothing in the phenomena of the circulation in these vessels which is inconsistent with its full operation. When the heart ceases its action, movements in the capillaries are sometimes due to the contractions of the arteries, an action which has already been fully described. Movements which have been observed in membranes detached from the body were undoubtedly due to the mere emptying of the divided vessels or to simple gravitation.

There is a circulation of the blood in the area vasculosa, the first blood-vessels that are developed before the heart is formed; but there are no definite and reliable observations which show that there is any regular movement of the blood, which can be likened to the circulation as it is observed after the development of the heart, anterior to the appearance of a contractile central organ. Another example of what is supposed to be circulation without the intervention of the heart is in cases of acardiac fœtuses. Monsters without a heart, which have undergone considerable development and which present systems of arteries, capillaries and veins, have been described. All of these, however, are accompanied by a twin, in which the development of the circulatory system is quite or nearly perfect.

*Influence of Temperature on the Capillary Circulation.*—Within moderate limits, a low temperature, produced by local applications, has been found to diminish the quantity of blood sent to the capillaries and retard the circulation, while a high temperature increases the supply of blood and accelerates its current. Poiseuille found that when a piece of ice was applied to the web of a frog's foot, the mesentery of a small warm-blooded animal or to any part in which the capillary circulation can be observed, the number of corpuscles circulating in the arterioles became very much diminished, "those which carried two or three rows of corpuscles giving passage to but a single row." The circulation in the capillaries first became slower and then entirely ceased in parts. On removing the ice, in a very few minutes the circulation regained its former characters. When, on the other hand, the part was covered with water at 104° Fahr. (40° C.), the rapidity of the current in the capillaries was so much increased that the form of the corpuscles could with difficulty be distinguished.

## Circulation of the Blood in the Veins.

The blood, distributed to the capillaries of all the tissues and organs by the arteries, is colected from these parts in the veins and carried back to the heart. In studying the anatomy of the capillaries or in observing the passage of the blood from the capillaries to larger vessels in parts of the living organism which can be submitted to microscopical examination, it is seen that the capillaries, vessels of nearly uniform diameter and anastomosing in every direction, empty into a system of vessels, which, by union with others, become larger and larger, and carry the blood away in a uniform current. These are called the venules, or venous radicles. They are the peripheral radicles of the vessels which carry the blood to the heart.

The venous system may be considered, in general terms, as divided into two sets of vessels; one, which is deep-seated and situated in proximity to the arteries, and the other, which is superficial and receives the greatest part of the blood from the cutaneous surface. The entire capacity of these vessels, as compared with that of the arteries, is very great. As a general rule, each vein, when fully distended, is larger than its adjacent artery. Many arteries are accompanied by two veins, as the arteries of the extremities; while certain of them, like the brachial or spermatic, have more than two. Added to these, are the superficial veins which have no corresponding arteries. It is true that some arteries have no corresponding veins, but examples of this kind are not sufficient in number to diminish, in any marked degree, the great preponderance of the veins, both in number and volume. It is impossible to give an accurate estimate of the extreme capacity of the veins as compared with the arteries, but it must be much greater. Borelli estimated that the capacity of the veins was to the capacity of the arteries, as 4 to 1; and Haller, as $2\frac{1}{4}$ to 1. The proportion is very variable in different parts of

FIG. 37.—*Venous radicles uniting to form a small vein, from the muscular coat of the urinary bladder of the frog; magnified* 400 *diameters* (from a photograph taken at the United States Army Medical Museum).

This preparation shows the endothelium of the vessels. It is injected with silver nitrate, stained with carmine and mounted in Canada balsam.

the body. In some situations the capacity of the veins and arteries is about equal; while in others, as in the pia mater, the veins will contain, when fully distended, six times as much as the arteries.

In attempting to compare the quantity of blood normally circulating in the veins with that contained in the arteries, such variations are found at different times and in different parts, both in the quantity of blood, rapidity of circulation, pressure etc., that a definite estimate is impossible. It would be unprofitable to attempt even an approximate comparison, as the variations in the venous circulation constitute one of its most important physiological peculiarities, which must be fully appreciated in order to form a just idea of the uses of the veins. The arteries are always full, and their tension is subject to comparatively slight variations. Following the blood into the capillaries, important modifications in the circulation are observed, with varying physiological conditions of the parts. As would naturally be expected, the condition of the veins varies with the changes in the capillaries from which the blood is received. In addition to this, there are independent variations, as in the erectile tissues, in the veins of the alimentary canal during absorption, in veins subject to pressure, etc.

Following the veins in their course, it is observed that anastomoses with each other form the rule, and not the exception, as in the arteries. There is always a number of channels by which the blood may be returned from a part; and if one vessel be obstructed from any cause, the current is simply diverted into another. The veins do not present a true anastomosing plexus, such as exists in the capillary system, but simply an arrangement by which the blood can readily find its way back to the heart, and by which the vessels may accommodate themselves to the frequent variations in the quantity of their fluid contents. This, with the peculiar valvular arrangement which exists in all but the veins of the cavities, provides against obstruction to the flow of blood through as well as from the capillaries, in which it seems essential to the proper nutrition and action of parts that the quantity and course of the blood should be regulated exclusively through the arterial system.

Collected by the veins from all parts of the body, the blood is returned to the right auricle, from the head and upper extremities by the superior vena cava, from the trunk and lower extremities, by the inferior vena cava, and from the substance of the heart, by the coronary veins.

*Structure and Properties of the Veins.*—The structure of the veins is more complex than that of the arteries. Their walls, which are always much thinner than the walls of the arteries, may be divided into a number of layers; but for convenience of physiological description, they may be regarded as presenting three distinct coats. These have properties which are somewhat distinctive for each, although not as much so as those of the three coats of the arteries.

The internal coat of the veins is a continuation of the single coat of the capillaries and of the internal coat of the arteries. It is a simple, homogeneous membrane, somewhat thinner than in the arteries, lined by a delicate layer of polygonal endothelium, the cells of which are shorter and broader than the endothelial cells of the arteries.

The middle coat is divided by some anatomists into two layers; an internal layer, which is composed chiefly of longitudinal fibres, and an external layer, in which the fibres have a circular direction. These two layers are intimately adherent and are quite closely attached to the internal coat. The longitudinal fibres are composed of connective-tissue fibres mingled with a large number of the smallest variety of the elastic fibres. This layer contains a large number of capillary vessels (vasa vasorum). The circular fibres are composed of elastic tissue, some of the fibres of the same variety as is found in the longitudinal layer, some of medium size, and some in the form of the "fenestrated membrane." In addition, there are inelastic fibres interlacing in every direction and mingled with capillary blood-vessels, and non-striated muscular fibres. In the human subject, in the veins of the central portion of the nervous system, the dura mater, the pia mater, the bones, the retina, the vena cava descendens, the thoracic portion of the vena cava ascendens, the external and internal jugulars and the subclavian veins, there are no muscular fibres in the middle coat. In the larger veins, such as the abdominal vena cava, the iliac, crural, popliteal, mesenteric and axillary veins, there are both longitudinal and circular fibres. In the smaller veins, the fibres are circular. In the smallest veins, the middle coat is composed of fine fibres of connective tissue with a very few muscular fibres.

The external coat of the veins is composed of ordinary fibrous tissue, like that of the corresponding coat of the arteries. In the largest veins, particularly those of the abdominal cavity, this coat contains a layer of longitudinal, non-striated muscular fibres. In the veins near the heart, are found a few striated fibres, which are continued on to the veins from the auricles. In some of the inferior animals, as the turtle, these fibres are quite thick, and pulsation of the veins in the immediate vicinity of the heart is very marked. In nearly all veins, the external coat is several times thicker than the internal coat. This is most marked in the larger veins, in which the middle coat, particularly the layer of muscular fibres, is very slightly developed.

The venous sinuses and the veins which pass through bony tissue have only the internal coat, to which are superadded a few longitudinal fibres, the whole being closely attached to the surrounding parts. As examples, may be mentioned the sinuses of the dura mater and the veins of the large bones of the skull. In the first instance, there is little more than the internal coat of the vein firmly attached to the surrounding layers of the dura mater. In the second instance, the same thin membrane is adherent to canals formed by a layer of compact bony tissue. The veins are much more closely adherent to the surrounding tissues than the arteries, particularly when they pass between layers of aponeurosis.

The peculiarities in the anatomy of the veins indicate considerable differences in their properties as compared with the arteries. When a vein is cut across, its walls fall together, if not supported by adhesions to surrounding tissues, so that its caliber is nearly or quite obliterated. The elastic tissue, which gives to the larger arteries their great thickness, is very scanty in the veins, and the thin walls collapse when not sustained by liquid in the interior of the vessels.

Although with much thinner and apparently weaker walls, the veins, as a rule, will resist a greater pressure than the arteries. Wintringham (1740) showed that the inferior vena cava of a sheep, just above the opening of the renal veins, was ruptured by a pressure of one hundred and seventy-six pounds (79·8 kilos.), while the aorta, at a corresponding point, yielded to a pressure of one hundred and fifty-eight pounds (71·7 kilos). The strength of the portal vein was even greater, supporting a pressure of nearly five atmospheres, bearing a relation to the vena cava of six to five; yet these vessels had hardly one-fifth the thickness of the arteries. In the lower extremities in the human subject, the veins are much thicker and stronger than in other situations, a provision against the increased pressure to which they are habitually subjected in the upright posture. Wintringham noticed a singular exception to the general rule just given. In the vessels of the glands and of the spleen, the strength of the arteries was much greater than that of the veins. The splenic vein gave way under a pressure of little more than one atmosphere, while the artery supported a pressure of more than six atmospheres.

The different influences to which the venous and arterial circulations are subject serve to indicate the physiological importance of the great difference in the strength of the two varieties of vessels. It is true that in the arteries the constant pressure is greater than in the veins; but it is nearly the same throughout the arterial system, and the great extent of the outlet at the periphery provides against any very great increase in pressure, so long as the blood is in a condition which enables it to pass into the capillaries. The muscular fibres of the left ventricle have but a limited power, and when the pressure in the arteries is sufficient, as it sometimes is in asphyxia, to close the aortic valves so firmly that the force of the ventricle will not open them, it can not be increased. At the same time, the pressure is being gradually relieved by the capillaries, through which the blood slowly filters even when completely unaërated. With the veins it is different. The blood has a comparatively restricted outlet at the heart and is received by the capillaries from all parts of the system. The vessels are provided with valves, which render a general backward action impossible. Thus, restricted portions of the venous system, from pressure in the vessels, increase of fluid from absorption, accumulation by force of gravity and other causes, may be subjected to great and sudden variations in pressure. The great strength of these vessels enables them ordinarily to suffei these variations without injury; although varicose veins in various parts present examples of the effects of repeated and continued distention.

The veins possess a considerable degree of elasticity, although this property is not so marked as it is in the arteries. If a portion of a vein distended with blood be included between two ligatures and a small opening be made in the vessel, the blood will be ejected with some force, and the vessel becomes much reduced in caliber.

It has been shown by direct experiment that the veins are endowed with the peculiar contractility characteristic of the action of the non-striated muscular fibres. On the application of electric or mechanical stimulation, they contract slowly and gradually, the contraction being followed by a correspondingly gradual relaxation. There is never any rhythmical or peristaltic movement in the veins, sufficient to assist the circulation. The only regular movements which occur are seen in the vessels in immediate proximity to the right auricle, which are provided with a few fibres similar to those which exist in the walls of the heart.

Nerves from the vaso-motor system have been demonstrated in the walls of the larger veins but have not been followed out to the smaller ramifications of the vessels.

*Valves of the Veins.*—In all parts of the venous system, except, in general terms, in the abdominal, thoracic and cerebral cavities, there exist little membranous, semilunar folds, resembling the aortic and pulmonic valves of the heart. When the valves are closed, their convexities look toward the periphery. In the great majority of instances, the valves exist in pairs, but they are occasionally, although very rarely in the human subject, found in groups of three. They are seldom if ever found in veins of a less diameter than one line (2·1 mm.). The valves are formed in part of the lining membrane of the veins, with fine fibres of connective tissue, elastic fibres and non-striated muscular fibres. There exists, also, a fibrous ring following the line of attachment of the valvular curtains to the vein, which renders the vessel much stronger and less dilatable here than in the intervals between the valves. The valves are most abundant in the veins of the lower extremities. They are generally situated just below the point where a small vein empties into one of larger size, so that the blood as it enters finds an immediate obstacle to passage in the wrong direction. The situation of the valves may be readily observed in any of the superficial veins. If the flow of blood be obstructed, little knots will be formed in the congested vessels, which indicate the position and action of the valves. When the vein is thus congested and knotted, if the finger be pressed along the vessel in the direction of the blood-current, a portion situated between two valves may be emptied of blood; but it is impossible to empty any portion of the vessel by pressing the blood in the opposite direction (Harvey). On slitting open a vein, it is easy to observe the shape, attachment and extreme delicacy of structure of the valves. When the vessel is empty or when fluid moves toward the heart, the valves are closely applied to the walls; but if liquid or air be forced in the opposite direction, they project into its caliber, and by the application of their free edges to each other, effectually prevent any backward current. When closed the application of their free edges form a line which runs across the vessel. It is found that in successive sets of valves, these lines are at right angles to each other, so that if, in one set, this line have a direction from before backward, in the sets above and below, the lines run from side to side (Fabricius).

There are certain exceptions to the general proposition that the veins of the great cavities are not provided with valves. Valves are found in the portal system of some of the inferior animals, as the horse. They do not exist, however, in this situation in the human subject. Generally, in following out the branches of the inferior vena cava, no valves are found until the crural vein is reached; but occasionally there is a double valve at the origin of the external iliac. In some of the inferior animals, there exists constantly a single valvular fold in the vena cava at the openings of the hepatic, and one at the opening of the renal vein. This is not constant in the human subject. Valves are found in the spermatic, but not in the ovarian veins. A single valvular fold has been described at the opening of the right spermatic into the vena cava. There are two valves in the azygos vein near its opening into the superior vena cava. There is a single valve at the orifice of the coronary vein. There are no valves at the openings of the brachio-cephalic into the superior vena cava; but there is a strong, double valve at the point where the internal jugular opens into the brachio-cephalic. Between this point and the capillaries of the brain, the vessels have no valves, except in very rare instances, when one or two are found in the course of the jugular.

In addition to the double, or more rarely triple valves which have just been described, there is another variety, found in certain parts, at the point where a tributary vein opens into a main trunk. This consists of a single fold, which is attached to the smaller vessel but projects into the larger. Its action is to prevent regurgitation, by the same mechanism as that by which the ileo-cæcal valve prevents the passage of matters from the large into the small intestine.

The veins are adapted to the return of blood to the heart in a comparatively slow and unequal current. Distention of certain portions is provided for; and the vessels are so protected with valves, that whatever influences the current must favor its flow in the direction of the heart.

*Course of the Blood in the Veins.*—The experiments of Hales and Sharpey, showing that defibrinated blood can be made to pass from the arteries into the capillaries and out at the veins by a pressure less than that which exists in the arterial system, and the observations of Magendie upon the circulation in the leg of a living dog, showing that ligation of the artery arrests the flow in the vein, have established the fact that the force exerted by the left ventricle is sufficient to account for the venous circulation. The heart must be regarded as the prime cause of the movement of blood in the veins. Regarding this as definitely ascertained, there remain to consider, in the study of the course of the blood in the veins, the character of the current, the influence of the vessels themselves, the question of the existence of forces which may assist the *vis a tergo* from the heart, and conditions which may interfere with the flow of blood.

As a rule, in the normal circulation, the flow of blood in the veins is continuous and uniform. The intermittent impulse of the heart, which progressively diminishes toward the periphery but is still felt even in the smallest arteries, is lost in the capillaries. Here, for the first time, the blood moves in a constant current; and as the pressure in the arteries is continually supplying fresh blood, that which has circulated in the capillaries is forced into the venous radicles in a steady stream. As the supply to the capillaries of different parts is regulated by the action of the small arteries, and as this supply is subject to great variations, there must necessarily be corresponding variations in the current in the veins and in the quantity of blood which these vessels receive. Consequently, the venous circulation is subject to very great variations due to irregularity in the supply of blood, aside from any action of the vessels themselves or any external disturbing influences.

It often happens that a vein becomes obstructed from some cause which is entirely physiological, such as the action of muscles. The great number of veins, as compared with the arteries, and their free communications with each other, provide that the current, under these conditions, is simply diverted, passing to the heart by another channel. When any part of the venous system is distended, the vessels react on the blood and exert a certain influence on the current, always pressing it toward the heart, for the valves oppose a flow in the opposite direction.

The intermittent action of the heart, which pervades the whole arterial system, is generally absorbed, as it were, in the passage of the blood through the capillaries; but when the arterioles of any part are very much relaxed, the cardiac impulse may extend to the veins. When the glands are pouring out their secretions, the quantity of blood which they receive is very much increased. It is then furnished to supply material for the secretion, and not exclusively for nutrition. If the vein be opened at such a time, it is found that the blood has not lost its arterial character, that the quantity which escapes is increased, and that the flow is in an intermittent jet, as from a divided artery (Bernard). This is due to the relaxed condition of the arterioles of the part, and the phenomenon thus observed constitutes the true venous pulse. What thus occurs in a restricted portion of the circulatory system may take place in all the veins, though in a less marked degree. Physicians have frequently noticed, after the blood has been flowing for some time in the operation of venesection, that the color changes from black to red and the stream becomes intermittent, often leading the operator to fear that he has pricked the artery. In all probability this is due to the relaxation of the arterioles as one of the effects of abstraction of blood, producing the same condition that has been noted in some of the glands during their activity.

*Pressure of Blood in the Veins.*—The pressure in the veins is always much less than in the arteries. It is very variable in different parts of the venous system and in the same part at different times. As a rule, it is in an inverse ratio to the arterial pressure. Whatever favors the passage of blood from the arteries into the capillaries has a tendency to diminish the arterial pressure, and as it increases the quantity of blood which passes into the veins, it must increase the venous pressure. The great capacity of the venous system, its frequent anastomoses and the presence of valves which may shut off a portion from the rest, are conditions which involve considerable variations in pressure in different vessels. It has been ascertained that as a rule, the pressure is greatest at the periphery and progressively diminishes in the direction of the heart. In an observation on the calf, Volkmann found that with a pressure of about 6·5 inches (165·1 mm.) of mercury in the carotid, the pressure in the metatarsal vein was 1·1 inch (28 mm.), and but 0·36 (9·1 mm.) in the jugular. Analogous results were obtained in the more recent experiments by Jacobson. Muscular effort has a marked influence on the force of the circulation in certain veins and produces an elevation in the pressure. As the reduced pressure in the veins is due in a measure to the great relative capacity of the venous system and the free communications between the vessels, it would seem that if it were possible to reduce the capacity of the veins in a part and force all the blood to pass to the heart by a single vessel corresponding to the artery, the pressure in this vessel would be greatly increased. Poiseuille has shown this to be the fact by the experiment of tying all the veins coming from a part, except one which had the volume of the artery by which the blood was supplied, forcing all the blood to return by this single channel. This being done, he found the pressure in the vein very much increased, becoming nearly equal to that in the artery.

*Rapidity of the Venous Circulation.*—It is impossible to fix upon any definite rate as representing the rapidity of the current of blood in the veins. It will be seen that various conditions are capable of increasing very considerably the rapidity of the flow in certain veins, and that under certain conditions, the current in some parts of the venous system is very much retarded. Undoubtedly, the general movement of blood in the veins is very much slower than in the arteries, from the fact that the quantity of blood is greater. If it be assumed that the quantity of blood in the veins is double that contained in the arteries, the general average of the current would be diminished one-half. Near the heart, however, the flow becomes more uniform and progressively increases in rapidity.

As the effect of the heart's action upon the venous circulation is subject to so many modifying influences through the small arteries and capillaries, and as there are other forces influencing the current, which are by no means uniform in their action, estimates of the general rapidity of the venous circulation or of the variations in different vessels must necessarily be very indefinite.

## Causes of the Venous Circulation.

In the veins the blood is farthest removed from the influence of the contractions of the left ventricle; and although these are felt, there are many other causes which combine to carry on the venous circulation, and many influences by which it is retarded or obstructed.

The great and uniform force which operates on the circulation in these vessels is the *vis a tergo*. Reference has been made to the entire adequacy of the arterial pressure, propagated through the capillaries, to account for the movement of blood in the veins, provided there be no great obstacles to the current. The other forces which concur to produce movement of blood in the veins are the following:

1. Muscular action, by which many of the veins are at times compressed, thus forcing the blood toward the heart, regurgitation being prevented by the action of the valves.

2. A suction force exerted by the action of the thorax in respiration, operating, however, only on the veins in the immediate neighborhood of the chest.

3. A possible influence from contraction of the coats of the vessels themselves. This is marked in the veins near the heart, in some of the inferior animals.

4. The force of gravity, which operates only on vessels which carry blood from above downward to the heart, and a slight suction force which may be exerted upon the blood in a small vein as it passes into a larger vessel in which the current is more rapid.

The obstacles to the venous circulation are: pressure sufficient to obliterate the caliber of a vessel, when, from the free communications with other vessels, the current is simply diverted into another channel; expiratory efforts; the contractions of the right side of the heart; and the force of gravity, which operates, in the erect posture, on the current in all excepting the veins of the head, neck and parts of the trunk above the heart.

*Influence of Muscular Contraction.*—That the action of muscles has considerable influence on the current of blood in the veins situated between them and in their substance, has long been recognized; and this action is so marked, that the parts of the venous system which are situated in the substance of muscles have been compared by Chassaignac to a sponge full of liquid, vigorously pressed by the hand. It must always be remembered, however, that although the muscles are capable of acting on the blood contained in veins in their substance with great vigor, the heart is fully competent to carry on the venous circulation without their aid; a fact which is exemplified in the venous circulation in paralyzed parts.

It has been shown by actual observations with the hæmadynamometer, that muscular action is capable of increasing the pressure in certain veins. Bernard found that the pressure in the jugular of a horse, in repose, was 1·4 inch (31·8 mm.); but the action of the muscles in raising the head increased it to a little more than five inches (127 mm.), or nearly four times. Such observations show at once the great variations in the current and the important influence of muscular contraction on the venous circulation.

In order that contractions of muscles shall assist the venous circulation, two conditions are necessary:

1. The contraction must be intermittent. This is always the case in the voluntary muscles. It is a view entertained by many physiologists that each muscular fibre relaxes immediately after its contraction, which is instantaneous, and that a certain period of repose is necessary before it can contract again. However this may be, it is well known that all active muscular contraction, as distinguished from the efforts necessary to maintain the body in certain ordinary positions, is intermittent and not very prolonged. Thus the veins, which are partly emptied by the compression, are filled again during the repose of the muscle.

2. There should be no possibility of a retrograde movement of the blood. This condition is fulfilled by the action of the valves. Anatomical researches have shown, also, that these valves are most abundant in veins situated in the substance of or between the muscles, and they do not exist in the veins of the cavities, which are not subject to the same kind of compression.

*Force of Aspiration from the Thorax.*—During the act of inspiration, the enlargement of the thorax, by depression of the diaphragm and elevation of the ribs, affects the movements of fluids in all the tubes in its vicinity. The air enters by the trachea and expands the lungs so that they follow the movements of the thoracic walls. The flow of blood into the great arteries is somewhat retarded, as is indicated by a diminution in the arterial pressure; and finally, the blood in the great veins passes to the heart with greater facility and in increased quantity. This last-mentioned phenomenon can be readily observed, when the veins are prominent, in profound or violent inspiration. The veins at the lower part of the neck are then seen to empty themselves of blood during inspiration, and they become distended during expiration, producing a sort of pulsation which is synchronous with respiration. This can always be observed after exposure of the jugular in the lower part of the neck in an inferior animal. Direct observations on the jugulars show conclusively that the influence of inspiration can not be felt much beyond these vessels. They are seen to collapse with each inspiratory act, a condition which limits this influence to the veins near the heart. The flaccidity of the walls of the veins will not permit the extended action of any suction force. In the circulation the veins are moderately distended with blood by the *vis a tergo*, and, to a certain extent, they are supported by connections with surrounding tissues, so that the force of aspiration is felt farther than in experiments on vessels removed from the body. The blood, as it approaches the thorax, impelled by other forces, is considerably accelerated in its flow; but it is evident that beyond a certain point, and that point very near the chest, ordinary aspiration has no influence, and violent efforts rather retard than favor the venous current.

In the liver the influence of inspiration becomes a very important element in the mechanism of the circulation. This organ presents a vascular arrangement which is exceptional. The blood, distributed by the arteries in a capillary plexus in the mucous membrane of the alimentary canal and in the spleen, instead of being returned directly to the heart by the veins, is collected into the portal vein, carried to the liver, and is there distributed in a second set of capillary vessels. It is then collected in the hepatic veins and carried by the vena cava to the heart. The three hepatic veins open into the inferior vena cava near the point where it passes the diaphragm, where the force of aspiration from the thorax would materially assist the current of blood. On following these vessels into the substance of the liver, it is found that their walls are so firmly adherent to the tissue of the organ, that when cut across, they remain patulous; and it is evident that they must remain open under all conditions. The thorax can therefore exert a powerful influence upon the hepatic circulation; for it is only the flaccidity of the walls of the vessels which prevents this influence from operating throughout the entire venous system. Although this must be a very important element in the production of the circulation in the liver, the fact that the blood circulates in this organ in the fœtus before any movements of the thorax take place shows that it is not essential.

A farther proof, if any were needed, of the suction force of inspiration is found in an accident which is not infrequent in surgical operations on the lower part of the neck. When the veins in this situation are kept open by a tumor or by induration of the surrounding tissues, an inspiratory effort has occasionally been followed by the entrance of air into the vessels, an accident which is likely to lead to the gravest results. This occurs only when a divided vein is kept patulous; and the accident proves both the influence of inspiration on liquids in the veins near the chest and its restriction to the vessels in this particular situation by the flaccidity of their walls.

The cause of death from air in the veins is purely mechanical. The air, finding its way to the right ventricle, is mixed with the blood in the form of minute bubbles and is carried into the pulmonary artery. Once in this vessel, it is impossible for it to pass through the capillaries of the lungs, and death by suffocation is the result, if the quantity of air be large. It is because no blood can pass through the lungs, that the left cavities of the heart are usually found empty.

Air injected into the arteries produces no such serious effects as air in the veins. It is arrested in the capillaries of certain parts and in the course of a short time is absorbed.

Aside from the pressure exerted by the contraction of muscles and the force of aspiration from the thorax, the influences which assist the venous circulation are very slight. There is a slight contraction in the venæ cavæ in the immediate proximity of the heart, which is much more extended in many of the lower vertebrate animals and may be mentioned as having an influence—very insignificant it is true—on the flow of blood from the great veins.

In the veins which pass from above downward, the force of gravity favors the flow of blood. This is seen by the turgescence of the veins of the neck and face when the head is kept for a short time below the level of the heart. If the arm be elevated above the head, the veins of the back of the hand will be much reduced in size, from the greater facility with which the blood passes to the heart, while they are distended when the hand is allowed to hang by the side and the blood has to rise against the force of gravity.

Some physiologists are of the opinion that the right ventricle exerts an active suction force during its diastole; but experiments on animals do not fully sustain this view, and if such a force be exerted, its effect upon the circulation, even in the veins near the heart, must be very slight. In the great irregularity in the rapidity of the circulation in different veins, it must frequently happen that a vessel empties its blood into another of larger size, in which the current is more rapid. In such an instance, as a physical necessity, the more rapid current in the large vein exerts a certain suction force on the fluid in the smaller vessel.

### Uses of the Valves of the Veins.

It is evident that the principal use of the valves of the veins is to present an obstacle to the reflux of blood toward the capillaries; and it remains only to study the conditions under which they are brought into action.

There are two distinct conditions under which the valves of the veins may be closed. One of them is the arrest of circulation, from any cause, in veins in which the blood has to rise against the force of gravity; and the other, compression of veins, from any cause—generally from muscular contraction—which tends to force the blood from the vessels compressed, into others, when the valves offer an obstruction to a flow toward the capillaries and necessitate a current in the direction of the heart. In the first of these conditions, the valves are antagonistic to the force of gravity, and when the caliber of any vessel is temporarily obliterated, they aid in directing the current into anastomosing vessels. It is but rarely, however, that they act thus in opposition to the force of gravity; and it is only when many of the veins of a part are simultaneously compressed that they aid in diverting the current. When a single vein is obstructed, it is not probable that the valves are necessary to divert the current into other vessels, for this would take place in obedience to the *vis a tergo;* but when many veins are obstructed in a dependent part and the avenues to the heart become insufficient, the valves divide the columns of blood, so that the pressure is equally distributed throughout the extent of the vessels. This is, however, but an occasional action of the valves; and it is evident that their influence is only to prevent the weight of the entire column of blood, in vessels thus obstructed, from operating on the smallest veins and the capillaries. It can not make the work of the heart, when the blood is again put in motion, any less than if the column were undivided, as this organ must have sufficient power to open successively each set of valves.

It is in connection with the intermittent compression of the veins that the valves have their principal and almost constant use. Their situation alone would lead to this supposition. They are found in greatest numbers throughout the muscular system, having been demonstrated in vessels one line (2·1 mm.) in diameter. They are also found in the upper parts of the body, where they certainly do not operate against the force of gravity; while they do not exist in the cavities, where the venous trunks are not subject to compression. It has already been made sufficiently evident that the action of muscles seconds most powerfully the contractions of the heart. The *vis a tergo* from the heart is, doubtless, generally sufficient to turn this influence of muscular compression from the capillary system, and the valves of the veins are open; but they stand ready, nevertheless, to oppose regurgitation.

In the action of muscles, the skin is frequently stretched over the part, and the cutaneous veins are somewhat compressed. This may be seen in the hand, by letting it hang by the side until the veins become somewhat swollen, and then contracting the muscles, when the skin will become tense and the veins are very much less prominent. Here the valves have an important action. The compression of the veins is much greater in the substance of and between the muscles than in the skin; but the blood is forced from the muscles into the skin, and the valves act to prevent it from taking a retrograde course.

A full consideration of the venous anastomoses belongs to descriptive anatomy. It is sufficient to state, in this connection, that they are very abundant and provide for a return of the blood to the heart by a number of channels. The azygos vein, the veins of the spinal canal and veins in the walls of the abdomen and thorax connect the inferior with the superior vena cava. Even the portal vein has been shown to have its communications with the general venous system. Thus, in all parts of the organism, temporary compression of a vein merely diverts the current into some other vessel, and permanent obliteration of a vein produces enlargement of communicating branches, which soon become sufficient to meet all the requirements of the circulation.

### Conditions which impede the Venous Circulation.

*Influence of Expiration.*—The influence of expiration on the circulation in the veins near the thorax is directly opposed to that of inspiration. As the act of inspiration has a tendency to draw the blood from these vessels into the chest, the act of expiration assists in forcing the blood out from the vessels of the thorax and opposes a flow in the opposite direction. The effect of prolonged and violent expiratory efforts is quite marked, these being followed by congestion of the veins of the face and neck and a sense of fullness in the head, which may become very distressing. The opposition to the venous current generally extends only to vessels in the immediate vicinity of the thorax, or it may be stated in general terms, to those veins in which the flow of blood is assisted by the movements of inspiration; but while the inspiratory influence is absolutely confined to a very restricted circuit of vessels, the obstructive influence of very violent and prolonged expiration may be extended very much farther, as is seen when the vessels of the neck, face and conjunctiva become congested in prolonged vocal efforts, blowing etc. The mechanism of this is not a mere reflux from the large trunks of the thoracic cavity. Were this the case, it would be necessary to assume an insufficiency of certain valves, which does not exist. In extreme congestion, reflux of blood may take place to a certain extent in the external jugular, for this vessel has but two valves, which are not competent to prevent regurgitation. The chief cause of congestion, however, is due, not to regurgitation, but to accumulation from the periphery and an obstruction to the flow of blood into the great vessels.

It is in the internal jugular that the influence of expiration is most important, both on account of its great size in the human subject, as compared with the other vessels, and the importance and delicacy of the parts from which it collects the blood. At the opening of this vessel into the innominate vein, is a pair of strong and perfect valves, which effectually close the orifice when there is a tendency to regurgitation. When the act of expiration arrests the onward flow in the veins near the thorax, these valves are closed and effectually protect the brain from congestion by regurgitation. The blood accumulates behind the valves, but the free communication of the internal jugular with the other veins of the neck relieves the brain from congestion, unless the effort be extraordinarily violent and prolonged.

The above remarks with regard to the influence of expiration are applicable to vocal efforts, violent coughing or sneezing, or any unusual muscular efforts, such as straining, in which the glottis is closed.

*Regurgitant Venous Pulse.*—In the inferior animals, such as the dog, if the external jugular be exposed, a distention of the vessel is seen to accompany each expiratory act. This is sometimes observed in the human subject when respiration is exaggerated, and has been called improperly the venous pulse. There is no sufficient obstacle to the regurgitation of blood from the thorax into the external jugular, and distinct pulsations, synchronous with the movements of respiration, may be produced in this way.

It is evident that there are various other conditions which may impede the venous circulation. Accidental compression may temporarily arrest the flow in any particular vein. When the whole volume of blood is materially increased, as after a full meal with copious ingestion of liquids, the additional quantity of blood accumulates chiefly in the venous system and proportionally diminishes the rapidity of the venous circulation.

The force of gravity also has an important influence. It is much more difficult for the blood to pass from below upward to the heart than to flow downward from the head and neck. The action of this is seen if comparison be made between the circulation in the arm elevated above the head and hanging by the side. In the one case the veins are readily emptied and contain but little blood, and in the other the circulation is more difficult and the vessels are moderately distended. The walls of the veins are thickest and the valves are most abundant in parts of the body which are habitually dependent. The influence of gravity is exemplified in the production of varicose veins in the lower extremities. This disease is frequently produced by occupations which require constant standing; but the exercise of walking, aiding the venous circulation, as it does, by the muscular effort, has no such tendency.

*Circulation in the Cranial Cavity.*—In the encephalic cavity there are certain peculiarities in the anatomy of some of the vessels, with exceptional conditions of the blood as regards atmospheric pressure, which have been regarded as capable of essentially modifying the circulation. In the adult the cranium is a closed, air-tight box, containing the incompressible cerebral substance, blood, lymph and the cephalo-rachidian fluid; and the blood is here under conditions widely different from those presented in other parts of the system. The venous passages in the brain, which correspond to the great veins of other parts, are in the form of sinuses between the folds of the dura mater and are but slightly dilatable. In the perfectly consolidated adult head the blood is not subjected to atmospheric pressure, as in other parts, and the semisolids and liquids which make up the encephalic mass can not increase in size in congestion and diminish in anæmia. Notwithstanding these conditions, the fact remains, that examinations of the vessels of the brain after death show great differences in the quantity of blood which they contain. The question then arises as to what is displaced to make room for the blood in congestion, and what supplies the place of the blood in anæmia. An anatomical peculiarity which has not yet been considered offers an explanation of these phenomena. Between the pia mater and the arachnoid of the brain and spinal cord there exists a liquid, the cephalo-rachidian fluid, which is capable of passing from the surface of the brain to the spinal canal and communicates with the fluid in the ventricles (Magendie). The communication between the cranial cavity and the spinal canal is very free. It is easy to see one of the physiological uses of this liquid. When the pressure of blood in the arteries going to the brain is increased or when there is an obstacle to its return by the veins, more or less congestion takes place, and the blood forces the liquid from the cranial into the spinal cavity. The reverse takes place when the supply of blood to the brain is diminished. The physiological action of all highly organized and vascular parts seems to require certain variations in the supply of blood; and there is no good reason to suppose that the brain, in its varied conditions of activity and repose, is an exception to this general rule.

Physiologists, even before the time of Haller, had noticed alternate movements of expansion and contraction in the brain, connected with the acts of respiration. This is observed in children before the fontanels are closed, and in the adult when the brain is exposed by an injury or a surgical operation. The movements are an expansion with the act of respiration, which, in violent efforts, is sometimes so considerable as to produce cerebral hernia, and contraction with inspiration. With the act of expiration the flow of blood in the arteries is favored and the current in the veins is retarded. If the effort be violent, the valve at the opening of the internal jugular may be closed. This act would produce an expansion of the brain, not from reflux by the veins, but from the fact that the flow into the chest is impeded, and the blood, while passing in more freely by the arteries, is momentarily confined. With inspiration the flow into the thorax is materially aided, and the brain is in some degree relieved of this expanding force.

*Circulation in Erectile Tissues.*—In the organs of generation of both sexes, there exists a tissue which is subject to increase in volume and rigidity when in a condition of what is called erection. The parts in which the erectile tissue exists are, in the male, the corpora cavernosa of the penis, the corpus spongiosum and the glans penis; and in the female, the corpora cavernosa of the clitoris, the gland of the clitoris and the bulb of the vestibule.

The vascular arrangement in erectile organs, of which the penis may be taken as the type, is peculiar and is not found in any other part of the circulatory system. Taking the penis as an example, the arteries, which have an unusually thick, muscular coat, after they have entered the organ, do not simply branch and divide dichotomously, as in most other parts, but send off large numbers of arborescent branches, which immediately become tortuous and are distributed in the cavernous and spongy bodies in anastomosing vessels, with but a single, thin, homogeneous coat, like the true capillaries. These vessels are larger, even, than the arterioles which supply them with blood, some having a diameter of $\frac{1}{25}$ to $\frac{1}{17}$ of an inch (1 to 1·5 mm.). The cavernous bodies have an external investment of strong, fibrous tissue of considerable elasticity, which sends bands, or trabeculæ, into the interior, by which it is divided up into cells. The trabeculæ are composed of fibrous tissue mixed with a large number of non-striated muscular fibres. These cells lodge the blood-vessels, which ramify in the tortuous manner already indicated and finally terminate in the veins. The anatomy of the corpora spongiosa is essentially the same, the only difference being that the fibrous envelope and the trabeculæ are more delicate and the cells are smaller.

Without going fully into the mechanism of erection, it may be stated in general terms that during sexual excitement, or when erection occurs from any cause, the thick, muscular walls of the arteries of supply relax and allow the arterial pressure to distend the capacious vessels lodged in the cells of the cavernous and spongy bodies. This produces the characteristic change in the volume and position of the organ. It is evident that erection depends upon the peculiar arrangement of the blood-vessels, and is not simply a congestion, such as could occur in any vascular part. During erection there is not a stasis of blood; but if it continue for any length of time, the quantity which passes out of the part by the veins must be equal to that which passes in by the arteries.

*Derivative Circulation.*—In some parts of the circulatory system, there exists a direct communication between the arteries and the veins, so that all the blood does not necessarily pass through the minute vessels which have been described as true capillaries. This peculiarity, which had been noted by Todd and Bowman, Paget and others, has been studied by Sucquet. By using a black, solidifiable injection, he found that there were certain parts of the upper and lower extremities and the head which became colored by the injection, while other parts were not penetrated. Following the vessels by dissection, he showed that in the upper extremity, the skin of the fingers and part of the palm of the hand, and the skin over the olecranon are provided with vessels of considerable size, which allowed the fluid injected by the axillary artery to pass directly into some of the veins, while in other parts the veins were entirely empty. Extending his researches to the lower extremity, he found analogous communications between the vessels in the knee, toes and parts of the sole of the foot. He also found communications in the nose, cheeks, lips, forehead and ends of the ears, parts which are particularly liable to changes in color from congestion of vessels. These observations have been in the main confirmed by the more recent researches of Hoyer. It is evident that under certain conditions a larger quantity of blood than usual may pass through these parts, without necessarily penetrating the true capillaries and thus exerting a modifying influence upon nutrition.

*Pulmonary Circulation.*—The vascular system of the lungs merits the name, which is frequently applied to it, of the lesser circulation. The right side of the heart acts simultaneously with the left, but is entirely distinct from it, and its muscular walls are very much less powerful. The pulmonary artery has thinner and more distensible coats than the aorta and distributes its blood to a single system of capillaries, situated very near the heart. In the substance of the lungs, the pulmonary artery is broken up into capillaries, most of them just large enough to allow the passage of the blood-corpuscles in a single row. These vessels are provided with a single coat and form a very close net-work surrounding the air-cells. From the capillaries the blood is collected by the pulmonary veins and conveyed to the left auricle. There is no great disparity between the arteries and veins of the pulmonary system as regards capacity. The pulmonary veins in the human subject are not provided with valves.

The blood in its passage through the lungs does not meet with the resistance which is presented in the systemic circulation; and the anatomy of the pulmonary vessels and of the right side of the heart shows that the blood must circulate in the lungs with comparative facility. The power of the right ventricle is evidently less than half that of the left, and the pulmonary artery will sustain a much less pressure than the aorta.

The two sides of the heart act simultaneously; and at the same time that the blood is sent by the left ventricle to the system it is sent by the right ventricle to the lungs. The pressure of blood in the pulmonary artery, measured by connecting a cardiometer with a trocar introduced into the pulmonary artery of a living horse through one of the intercostal spaces, has been found to be about one-third as great as the pressure in the aorta, which corresponds pretty nearly with an estimate of the comparative power of the two ventricles, judging from the thickness of their muscular walls (Chauveau and Faivre).

On microscopical examination of the circulation in the lower animals, as the frog, the movement of blood in the capillaries of the lungs does not present any differences from the capillary circulation in other parts, except that the vessels seem more crowded with corpuscles and there is no "still layer" next their walls.

*Circulation in the Walls of the Heart.*—The circulation in the walls of the heart does not present any important peculiarities. It has been shown that the pressure of blood in the coronary arteries in the dog, during the ventricular systole, is sufficient to supply the arterioles in the substance of the heart with blood precisely as it is supplied to the general arterial system. In a number of experiments, in which simultaneous traces of the pulse-beats were obtained, it has been found that the coronary and carotid pulses were practically synchronous (Martin).

*Passage of the Blood-Corpuscles through the Walls of the Vessels* (*Diapedesis*).—In the frog it has been observed that the leucocytes sometimes pass through the walls of the blood-vessels, either by means of small orifices (stromata) or by a kind of filtration through the substance which unites the borders of the endothelial cells. This phenomenon was described by Waller, in 1841, but has attracted much attention since the more recent researches of Cohnheim. In this process it is observed that the leucocytes, which first adhere to the vascular walls, send out little projections which penetrate the membrane, so that a point appears on the outside of the vessel. This point becomes larger and larger, until the entire mass of the corpuscle has passed through. The corpuscles then migrate a certain distance by means of the movements known as amœboid, which have already been described. It was supposed by Cohnheim that this was one of the early phenomena of inflammation, the migrating corpuscles afterward multiplying by division, constituting the so-called pus-corpuscles. Following stasis of blood in the small vessels, the red corpuscles, it is supposed, pass out in the same way. It is not certain that diapedesis, even of leucocytes, is a normal process or that it takes place in the human subject. According to Hering, the red corpuscles pass through the walls of the vessels, only when the pressure is sufficient to produce transudation of the blood-plasma.

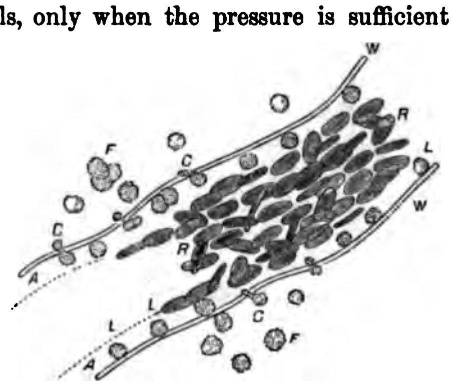


FIG. 88.—*Small blood-vessel of the mesentery of the frog, showing diapedesis of leucocytes* (Landois). W, W, walls of the vessel; A, A, still layer; R, R, red blood-corpuscles; L, L, leucocytes in contact with the wall, C, C, in different stages of diapedesis; F, F, leucocytes that have passed out of the vessel.

RAPIDITY OF THE CIRCULATION.

Several questions of considerable physiological importance arise in connection with the general rapidity of the circulation:

1. What length of time is occupied in the passage of the blood through both the lesser and the greater circulations?

2. What is the time required for the passage of the entire mass of blood through the heart?

3. What influence has the number of pulsations of the heart on the general rapidity of the circulation?

The first of these questions is the one which has been most satisfactorily answered by experiments on living animals. In 1827, Hering made the experiment of injecting into the jugular vein of a living animal a solution of potassium ferrocyanide, noting the time which elapsed before it could be detected in the blood of the vein of the opposite side. This gave the first correct idea of the rapidity of the circulation. He drew the blood at intervals of five seconds after beginning the injection, and thus, by repeated observations, ascertained pretty nearly the rapidity of a circuit of blood in the animals upon which he experimented. Vierordt (1858) collected the blood as it flowed, in little vessels fixed on a disk revolving at a known rate, which gave more exactness to the observations. The results obtained by these two observers were nearly identical.

The only objection which could be made to these experiments is that a saline solution, introduced into the circulation, would have a tendency to diffuse itself throughout the whole mass of blood, it might be, with considerable rapidity. This certainly is an element which should be taken into account; but from the definite data which have been obtained concerning the rapidity of the arterial circulation and the inferences which are unavoidable with regard to the rapidity of the venous circulation, it would seem that the saline solution must be carried on by the mere rapidity of the arterial flow to the capillaries, which are very short, taken up from them, and carried on by the veins, and thus through the entire circuit, before it has had time to diffuse itself to any considerable extent. It is not apparent how this objection can be overcome, for a substance must be used which will mix with the blood; otherwise it could not pass through the capillaries.

There seems no reason why, with the above restrictions, the results obtained by Hering should not be accepted and their application be made to the human subject.

Hering found that the rapidity of the circulation in different animals had an inverse ratio to their size and a direct ratio to the rapidity of the action of the heart.

The following are the mean results in certain of the domestic animals, taking the course from jugular to jugular, when the blood passes through the lungs and through the capillaries of the face and head:

| | | | | |
|---|---|---|---|---|
| In the Horse, | the circulation | is accomplished in | 27·3 | seconds. |
| " Dog, | " | " | 15·2 | " |
| " Goat, | " | " | 12·8 | " |
| " Rabbit, | " | " | 6·9 | " |

Applying these results to the human subject and taking into account the size of the body and the rapidity of the heart's action, the duration of the circuit from one jugular to the other may be estimated at 21·4 seconds, and the general average through the entire system, at 23 seconds. This estimate is simply approximate; but the results in the inferior animals may be received as very nearly accurate.

Estimates of the time required for the passage of the whole mass of blood through the heart are even less definite than the estimate of the general rapidity of the circulation. To arrive at any satisfactory result, it is necessary to know the entire quantity of blood in the body and the exact quantity which passes through the heart at each pulsation. If the whole mass of blood be divided by the quantity discharged from the heart with each ventricular systole, the result gives the number of pulsations required for the passage of the whole mass of blood through the heart; and knowing the number of beats per minute, the length of time thus occupied is ascertained. The objection to this kind of estimate is the inaccuracy of the data respecting the quantity of blood in the system as well as the quantity which passes through the heart with each pulsation. Nevertheless, an estimate can be made, which, if it be not entirely accurate, can not be very far from the truth.

The entire quantity of blood, according to estimates which seem to be based on the most reliable data, is about one-tenth the weight of the body, or fourteen pounds (6·35 kilos.), in a man weighing one hundred and forty pounds (63·5 kilos.). The quantity discharged at each ventricular systole is estimated by Valentin at five ounces (141·7 grammes), and by Volkmann, at six ounces (170·1 grammes). Assuming that at each systole, the left ventricle discharges all its blood, except perhaps a few drops, and that this quantity in an ordinary-sized man is five ounces (141·7 grammes), it would require forty-five pulsations for the passage through the heart of the entire mass of blood. Assuming the pulsations to be seventy-two per minute, this would occupy thirty-seven and a half seconds.

The relation of the rapidity of the circulation to the frequency of the heart's action is a question which was not neglected in the experiments of Hering. It is evident that if the charge of blood sent into the arteries be the same, or nearly the same, under all conditions, any increase in the number of pulsations of the heart would produce a corresponding acceleration of the general current of blood. This is a proposition, however, which can not be taken for granted; and there are many facts which favor a contrary opinion. It may be stated as a general rule, that when the acts of the heart increase in frequency they diminish in force; and this renders it probable that the ventricle is most completely distended and emptied when its action is moderately slow. When, however, the pulse is very much accelerated, the increased number of pulsations of the heart might be sufficient to overbalance the diminished force of each act and would thus actually increase the rapidity of the circulation. In observations made on horses, by increasing the frequency of the pulse, on the one hand, physiologically, by exercise, and on the other hand, pathologically, by producing inflammatory action, it is shown that when the pulse is accelerated in inflammation, the value of the contractions of the heart, as represented by the quantity of blood discharged, bears an inverse ratio to their number and is so much diminished as absolutely to produce a current of less rapidity than normal. In the physiological increase in the rate of the pulse by exercise, there was a considerable increase in the actual rapidity of the circulation (Hering).

With regard to the relations between the rapidity of the heart's action and the general rapidity of the circulation, the following conclusions may be given as the results of experimental inquiry:

1. In physiological increase in the number of beats of the heart, as the result of exercise, for example, the general circulation is somewhat increased in rapidity, though not in proportion to the increase in the rapidity of the pulse.

2. In pathological increase in the rapidity of the heart's action, as in febrile movement, the rapidity of the general circulation is generally diminished, it may be, to a very great extent.

3. Whenever the number of beats of the heart is considerably increased from any cause, the quantity of blood discharged at each ventricular systole is very much diminished, either from lack of complete distention or from imperfect emptying of the cavities.

*Phenomena in the Circulatory System after Death.*—Nearly every autopsy shows that after death, the blood does not remain equally distributed in the arteries, capillaries and veins. Influenced by gravitation, it accumulates in and discolors the most dependent parts of the body. The arteries are always found empty, and all the blood in the body accumulates in the venous system and capillaries; a fact which was observed by the ancients and gave rise to the belief that the arteries were air-bearing tubes. This is readily explained by the post-mortem contraction of the muscular coat of the arteries. If the artery and vein of a limb be exposed in a living animal and all the other vessels be tied, compression of the artery does not immediately arrest the current in the vein, but the blood will continue to flow until the artery is entirely emptied (Magendie). The artery, when relieved from the distending force of the heart, reacts on its contents by virtue of its contractile coat and completely empties itself of blood. An action similar to this takes place throughout the arterial system after death. The vessels react on their contents and gradually force all the blood into and through the capillaries, which are very short, to the veins, which are capacious, distensiblé and but slightly contractile. This begins immediately after death while the contractility of the muscular coat of the arteries remains, and is seconded by the subsequent cadaveric rigidity, which affects all the involuntary as well as the voluntary muscular fibres. Once in the venous system, the blood can not return on account of the valves. Thus, after death, the blood is found in the veins and capillaries of dependent parts of the body.

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## CHAPTER IV.

### *RESPIRATION—RESPIRATORY MOVEMENTS.*

General considerations—Physiological anatomy of the respiratory organs—Movements of respiration—Inspiration—Muscles of inspiration—Expiration—Muscles of expiration—Types of respiration—Frequency of the respiratory movements—Relations of inspiration and expiration to each other—Respiratory sounds—Capacity of the lungs and the quantity of air changed in the respiratory acts—Residual air—Reserve air—Tidal, or breathing air—Complemental air—Extreme breathing capacity—Relations in volume of the expired to the inspired air—Diffusion of air in the lungs.

THE characters of the blood are by no means identical in the three great divisions of the vascular system; but physiologists have thus far been able to investigate only the differences which exist between arterial and venous blood, for the capillaries are so short, communicating directly with the arteries on the one side and the veins on the other, that it is impossible to obtain a specimen of true capillary blood. In the capillaries, however, the nutritive fluid, which is identical in all parts of the arterial system, undergoes changes which render it unfit for nutrition. Thus modified it is known as venous blood; and the only office of the veins is to carry it back to the right side of the heart, to be sent to the lungs, where it loses the vitiating substances it has collected in the tissues, takes in a fresh supply of oxygen and goes to the left, or systemic heart, again prepared for nutrition. As the processes of nutrition vary in different parts of the organism, there are of necessity corresponding variations in the composition of the blood in different veins.

The important substances that are given off by the lungs are exhaled from the blood; and the gas which disappears from the air is absorbed by the blood, mainly by the red corpuscles.

A proper supply of oxygen is indispensable to nutrition and even to the comparatively mechanical process of circulation; but it is no less necessary to the nutritive processes that carbon dioxide, which the blood acquires in the tissues, should be removed.

Respiration may be defined strictly as the process by which the various tissues and organs receive and appropriate oxygen.

As it is almost exclusively through the blood that the tissues and organs are supplied with oxygen, and as the blood receives and exhales most of the carbon dioxide, the respiratory process in the lungs may be said to consist chiefly in the change of venous into arterial blood; but experiments have demonstrated that the tissues themselves, detached from the body and placed in an atmosphere of oxygen, will absorb this gas and exhale carbon dioxide. Under these conditions they certainly respire; and it is evident, therefore, that in this process, the intervention of the blood is not an absolute necessity.

The tide of air in the lungs does not strictly constitute respiration. These organs merely serve to facilitate the introduction of oxygen into the blood and the exhalation of carbon dioxide. If the system be drained of blood or if the blood be rendered incapable of interchanging its gases with the air, respiration ceases, and all the phenomena of asphyxia are presented, although air be introduced into the lungs with perfect regularity. It must be remembered that the essential processes of respiration take place in all the tissues and organs of the system and not in the lungs. Respiration is a process similar to what are known as the processes of nutrition; and although it is much more active and uniform than are the ordinary nutritive changes, it is inseparably connected with and strictly a part of the general process. As in the nutrition of the tissues the nitrogenized constituents of the blood, united with inorganic substances, are transformed into the tissue itself, finally changed into excrementitious products, such as the urinary matters, and discharged from the body, so the oxygen of the blood is appropriated, and carbon dioxide, which is an excrementitious substance, is produced, whenever tissues are worn out and regenerated. There is a necessary and inseparable connection between all these processes; and they must be considered, not as distinct in themselves, but as different parts of the general function of nutrition.

As physiologists are unable to follow out all the intermediate changes which take place between the appropriation of nutritive materials from the blood and the production of effete, or excrementitious substances, it is impossible to say precisely how oxygen is used by the tissues and how carbon dioxide is produced. It is known only that more or less oxygen is necessary to the nutrition of all tissues, in all animals, high or low in the scale, and that the tissues produce a certain quantity of carbon dioxide. The fact that oxygen is consumed with much greater rapidity than any other nutritive substance and that the production of carbon dioxide is correspondingly active, as compared with other effete products, points to a connection between the absorption of the one and the production of the other.

The essential conditions for respiration in animals which have a circulating nutritive fluid are air and blood separated by a membrane which will allow the passage of gases. The effete products of respiration contained in the blood, the most important of which is carbon dioxide, pass out and vitiate the air. The air is deprived of a certain portion of its oxygen, which passes into the blood, to be conveyed to the tissues. Thus the air must be changed to supply fresh oxygen and get rid of the carbon dioxide. The rapidity of this change is in proportion to the nutritive activity of the animal and the rapidity of the circulation of the blood.

## Physiological Anatomy of the Respiratory Organs.

Passing backward from the mouth to the pharynx, two openings are observed; a posterior opening, which leads to the œsophagus, and an anterior opening, the opening of the larynx, which is the beginning of the passages concerned exclusively in respiration.

Beginning with the larynx, it is seen that the cartilages of which it is composed are sufficiently rigid and unyielding to resist the pressure produced by any inspiratory effort. Across its superior opening are the vocal chords, which are four in number and have a direction from before backward. The two superior are called the false vocal chords, because they are not concerned in the production of the voice. The two inferior are the true vocal chords. They are ligamentous bands covered by folds of mucous membrane, which is

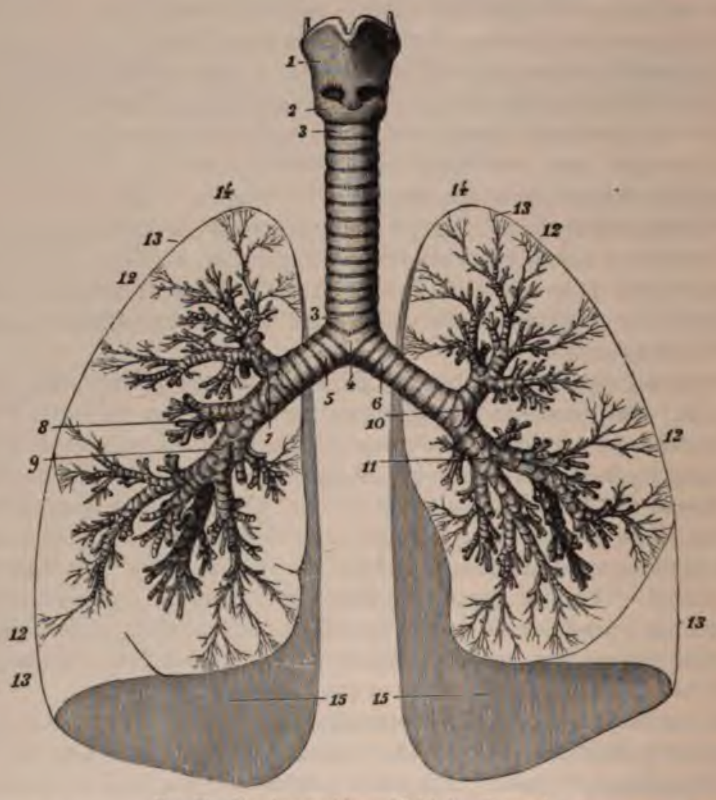


Fig. 39.—*Trachea and bronchial tubes* (Sappey).

1, 2, larynx; 3, 3, trachea; 4, bifurcation of the trachea; 5, right bronchus; 6, left bronchus; 7, bronchial division to the upper lobe of the right lung; 8, division to the middle lobe; 9, division to the lower lobe; 10, division to the upper lobe of the left lung; 11, division to the lower lobe; 12, 12, 12, 12, ultimate ramifications of the bronchia; 13, 13, 13, 13, lungs, represented in contour; 14, 14, summit of the lungs; 15, 15, base of the lungs.

quite thick on the superior chords and very thin and delicate on the true vocal chords. These bands are attached anteriorly to a fixed point between the thyroid cartilages, and posteriorly, to the movable arytenoid cartilages. Air is admitted to the trachea through an opening between the chords, which is called the rima glottidis. Little muscles, arising from the thyroid and cricoid and attached to the arytenoid cartilages, are capable of separating and approximating the points to which the vocal chords are attached posteriorly, so as to open and close the rima glottidis.

If the glottis be exposed in a living animal, certain regular movements are presented, which are synchronous with the acts of respiration. The larynx is slightly opened at each inspiration, by the action of the muscles referred to above, so that the air has a free entrance to the trachea. At the termination of the inspiratory act these muscles are relaxed, the vocal chords fall together by their own elasticity, and in expiration, the chink of the glottis returns to the condition of a narrow slit. The expulsion of air from the lungs in tranquil respiration is a passive process and tends in itself to separate the vocal chords; but inspiration, which is active, were it not for the movements of the glottis, would have a tendency to draw the vocal chords together. The muscles which are concerned in producing these movements are animated by the inferior laryngeal branches of the pneumogastric nerves. The respiratory movements of the larynx are entirely distinct from those concerned in the production of the voice.

Attached to the anterior portion of the larynx, is the epiglottis, a little, leaf-shaped lamella of fibro-cartilage, which, during ordinary respiration, projects upward and lies against the posterior portion of the tongue. During the act of deglutition, respiration is momentarily interrupted, and the air-passages are protected by the tongue, which presses backward, carrying the epiglottis before it and completely closing the opening of the larynx. Physiologists have questioned whether the epiglottis be necessary to the complete protection of the air-passages; and it has frequently been removed from the lower animals without apparently interfering with the proper deglutition of solids or liquids (Magendie). It is a question, however, whether the results of this experiment can be absolutely applied to the human subject. In a case of loss of the entire epiglottis, which was observed in the Bellevue Hospital, the patient experienced slight difficulty in swallowing, from the passage of little particles into the larynx, which produced cough. This case, and others of a similar character which are on record, show that the presence of the epiglottis, in the human subject at least, is necessary to the complete protection of the air-passages in deglutition.

Passing down the neck from the larynx toward the lungs, is the trachea, which is four to four and a half inches (10·16 to 11·43 centimetres) in length and about three-quarters of an inch (19·1 mm.) in diameter. It is provided with cartilaginous rings, sixteen to twenty in number, which partially surround the tube, leaving about one-third of its posterior portion occupied by fibrous tissue mixed with a certain number of non-striated muscular fibres. Passing into the chest, the trachea divides into the two primitive bronchia, the right being shorter, larger and more horizontal than the left. These tubes, provided, like the trachea, with imperfect cartilaginous rings, enter the lungs, divide and subdivide, until the minute ramifications of the bronchial tree open directly into the air-cells. After penetrating the lungs, the carti-

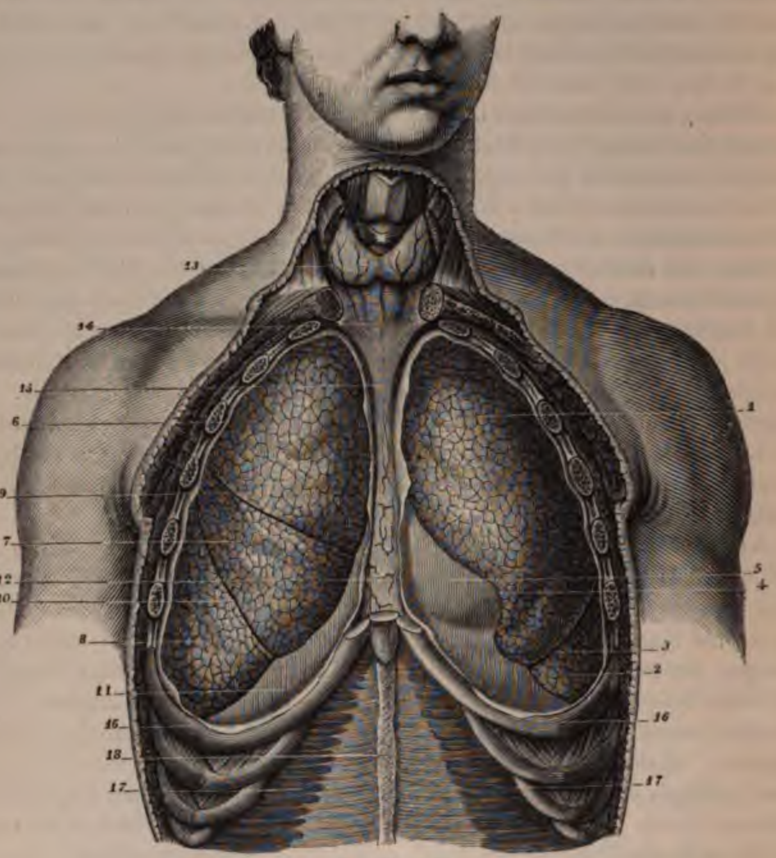

FIG. 40.—*Lungs, anterior view* (Sappey).

1, *upper lobe of the left lung*; 2, *lower lobe*; 3, *fissure*; 4, *notch corresponding to the apex of the heart*; 5, pericardium: 6, *upper lobe of the right lung*; 7, *middle lobe*; 8, *lower lobe*; 9, *fissure*; 10, *fissure*; 11, diaphragm; 12, anterior mediastinum; 13, thyroid gland; 14, middle cervical aponeurosis; 15, process of attachment of the mediastinum to the pericardium; 16, 16, seventh ribs; 17, 17, transversales muscles; 18, linea alba.

lages become irregular and are in the form of oblong, angular plates, which are so disposed as to completely encircle the tubes. In tubes of very small size, these plates are fewer than in the larger bronchia, until, in tubes of a less diameter than $\frac{1}{50}$ of an inch (0·5 mm.), they disappear.

The walls of the trachea and bronchial tubes are composed of two distinct membranes; an external membrane, between the layers of which the cartilages are situated, and a lining, mucous membrane. The external membrane is composed of inelastic and elastic fibrous tissue. Posteriorly, in the space not covered by cartilaginous rings, these fibres are mixed with a certain number of non-striated muscular fibres, which exist in two layers; a thick, internal layer, in which the fibres are transverse, and a thinner, longitudinal layer, which is external. The collection of muscular fibres in the posterior part of the trachea is sometimes called the trachealis muscle. Throughout the bronchial tubes, there are circular fasciculi of non-striated muscular fibres lying just beneath the mucous membrane, with a number of longitudinal elastic fibres. The character of the bronchia abruptly changes in tubes less than $\frac{1}{50}$ of an inch (0·5 mm.) in diameter. They then lose the cartilaginous rings, and the external and the mucous membranes become so closely united that they can no longer be separated by dissection. The circular muscular fibres continue as far as the air-cells. The mucous membrane is smooth, covered by ciliated epithelium, the movements of the cilia being always from within outward, and it is provided with mucous glands. These glands are of the racemose variety and in the larynx they are of considerable size. In the trachea and bronchia, racemose glands exist in the membrane on the posterior surface of the tubes; but anteriorly are small follicles, terminating in a single, and sometimes a double, blind extremity. These follicles are lost in tubes measuring less than $\frac{1}{50}$ of an inch (0·5 mm.) in diameter.

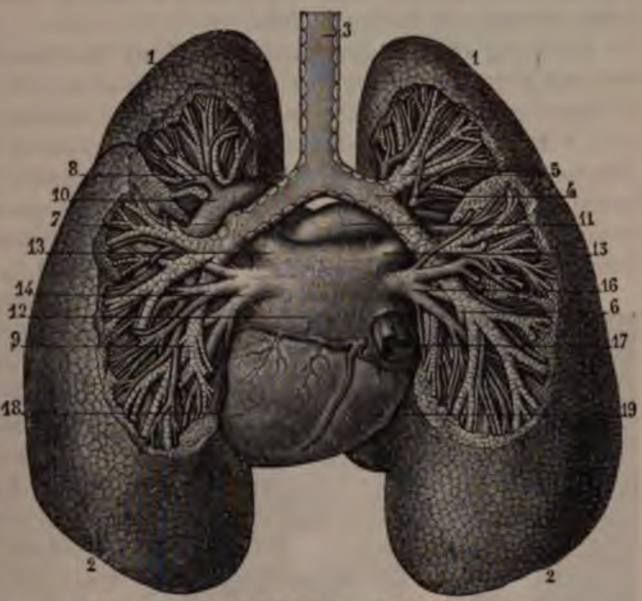


FIG. 41.—*Bronchia and lungs, posterior view* (Sappey).

1, 1, *summit of the lungs*; 2, 2, *base of the lungs*; 3, *trachea*; 4, *right bronchus*; 5, *division to the upper lobe of the lung*; 6, *division to the lower lobe*; 7, *left bronchus*; 8, *division to the upper lobe*; 9, *division to the lower lobe*; 10, left branch of the pulmonary artery; 11, right branch; 12, left auricle of the heart; 13, left superior pulmonary vein; 14, left inferior pulmonary vein; 15, right superior pulmonary vein; 16, right inferior pulmonary vein; 17, inferior vena cava; 18, left ventricle of the heart; 19, right ventricle.

When moderately inflated, the lungs have the appearance of irregular cones, with rounded apices, and concave bases resting upon the diaphragm. They fill that part of the cavity of the thorax which is not occupied by the heart and great vessels, and are completely separated from each other by the mediastinum. The lungs are in contact with the thoracic walls, each lung being covered by a reflection of the serous membrane which lines the cavity of the corresponding side. Thus they necessarily follow the movements of expansion and contraction of the thorax. Deep fissures divide the right lung into three lobes and the left lung into two. The surface of the lungs is divided into irregularly polygonal spaces, $\frac{1}{4}$ of an inch to an inch (6·4 to 25·4 mm.) in diameter, which mark what are sometimes called the pulmonary lobules; although this term is incorrect, as each of these divisions includes quite a number of the true lobules.

Following out the bronchial tubes from the diameter of $\frac{1}{50}$ of an inch (0·5 mm.), the smallest, which are $\frac{1}{120}$ to $\frac{1}{75}$ of an inch (0·21 to 0·33 mm.) in diameter, open into a collection of oblong vesicles, which are the air-cells. Each collection of vesicles constitutes one of the true pulmonary lobules and is $\frac{1}{50}$ to $\frac{1}{12}$ of an inch (0·5 to 2·1 mm.) in diameter. After entering the lobule, the tube forms a tortuous central canal, sending off branches which terminate in groups of eight to fifteen pulmonary cells. The cells are a little deeper than they are wide and have each a rounded, blind extremity. Some are smooth, but many are marked by little circular constrictions, or rugæ. In the healthy lung of the adult, after death, they measure $\frac{1}{200}$ to $\frac{1}{120}$ or $\frac{1}{70}$ of an inch (0·125 to 0·21 or 0·36 mm.) in diameter, but are capable of very great distention. The smallest cells are in the deep portions of the lungs, and the largest are situated near the surface. There are considerable variations in the size of the cells at different periods of life. The smallest cells are found in young children, and they progressively increase in size with age. The walls of the air-cells contain very abundant small, elastic fibres, which do not form distinct bundles for each air-cell, but anastomose freely with each other, so that the same fibres belong to two or more cells. This structure is peculiar to the parenchyma of the lungs and gives to these organs their great distensibility and elasticity, properties which play an important part in expelling the air from the chest, as a consequence simply of cessation of the action of the inspiratory muscles. Interwoven with these elastic fibres, is the richest plexus of capillary blood-vessels found in the economy. The vessels are larger than the capillaries in other situations, and the plexus is so close that the spaces between them are narrower than the vessels themselves. When distended, the blood-vessels form the greatest part of the walls of the cells.

FIG. 42.—*Mould of a terminal bronchus and a group of air-cells moderately distended by injection, from the human subject* (Robin).

Lining the air-cells, are very thin cells of flattened epithelium, $\frac{1}{2500}$ to

$\frac{1}{2000}$ of an inch (10 to 12·5 $\mu$), in diameter, which are applied directly to the walls of the blood-vessels. The epithelium here does not seem to be regularly desquamated as in other situations. Examination of injected specimens shows that the blood-vessels are so situated between the cells, that the blood in the greater part of their circumference is exposed to the action of the air.

The entire mass of venous blood is distributed in the lungs by the pulmonary artery. Arterial blood is conveyed to these organs by the bronchial arteries, which ramify and subdivide on the bronchial tubes and follow their course into the lungs, for the nourishment of these parts. It is possible that the tissue of the lungs may receive some nourishment from the blood of the pulmonary artery; but as this vessel does not send any branches to the

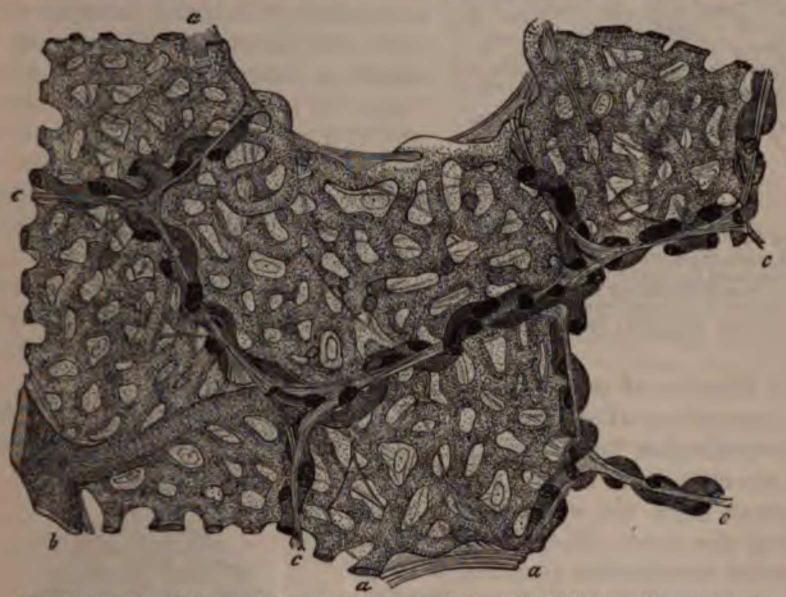


FIG. 43.—*Section of the parenchyma of the human lung, injected through the pulmonary artery* (Schulze).
*a*, *a*, *c*, *c*, walls of the air-cells; *b*, small arterial branch.

bronchial tubes, the bronchial arteries supply the matters for their nutrition and for the secretion of the mucous glands.

The foregoing anatomical sketch shows the adaptation of the trachea and bronchial tubes to the passage of the air by inspiration to the deep portions of the lungs, and the favorable conditions which it there meets with for an interchange of gases. It is also evident, from the great number of air-cells, that the respiratory surface must be very large, although it is impossible to form an accurate estimate of its extent.

## MOVEMENTS OF RESPIRATION.

In man and in the warm-blooded animals generally, inspiration takes place as a consequence of enlargement of the thoracic cavity and the entrance of a quantity of air through the respiratory passages, corresponding to the increased capacity of the lungs. In the mammalia, the chest is enlarged by the action of muscles; and in ordinary respiration, inspiration is an active process, while ordinary expiration is passive.

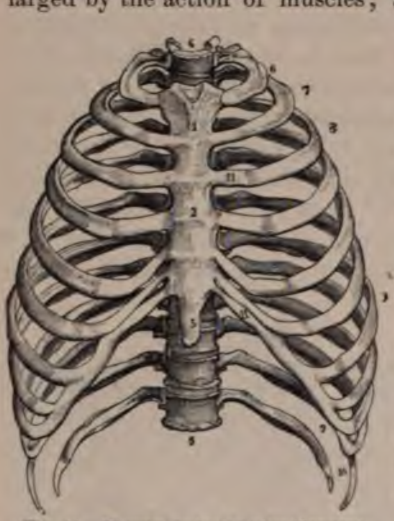

FIG. 44.—*Thorax, anterior view* (Sappey).
1, 2, 3, sternum; 4, circumference of the upper portion of the thorax; 5, circumference of the base of the thorax; 6, first rib; 7, second rib; 8, 8, last five sternal ribs; 9, upper three false ribs; 10, last two, or floating ribs; 11, costal cartilages.

A glance at the physiological anatomy of the thorax in the human subject makes it evident that the action of certain muscles will considerably increase its capacity. In the first place, the diaphragm mounts up into its cavity in the form of a vaulted arch. By contraction of its fibres, it is brought nearer a plane, and thus the vertical diameter of the thorax is increased. The walls of the thorax are formed by the dorsal vertebræ and ribs posteriorly, by the upper ten ribs laterally, and by the sternum and costal cartilages anteriorly. The direction of the ribs, their mode of connection with the sternum by the costal cartilages, and their articulation with the vertebral column, are such that by their movements, the antero-posterior and transverse diameters of the chest may be considerably modified.

*Inspiration.*—The ribs are somewhat twisted upon themselves and have a general direction forward and downward. The first rib is nearly horizontal, but the obliquity of the ribs progressively increases from the upper to the lower part of the chest. They are articulated with the bodies of the vertebræ, so as to allow of considerable motion. The upper seven ribs are attached by the costal cartilages to the sternum, these cartilages running upward and inward. The cartilages of the eighth, ninth and tenth ribs are joined to the cartilage of the seventh. The eleventh and twelfth are floating ribs and are attached only to the vertebræ.

It may be stated in general terms that inspiration is effected by descent of the diaphragm and elevation of the ribs; and expiration, by elevation of the diaphragm and descent of the ribs.

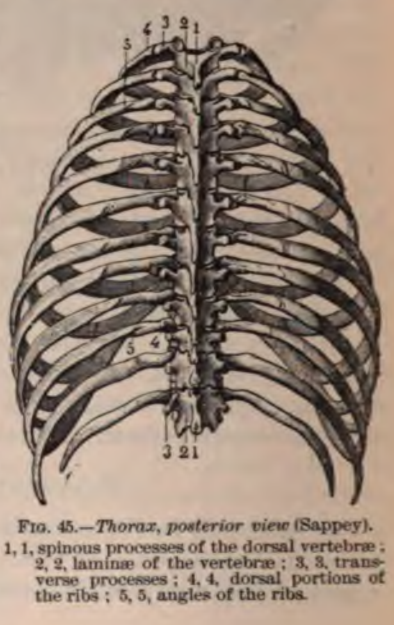

FIG. 45.—*Thorax, posterior view* (Sappey).
1, 1, spinous processes of the dorsal vertebræ; 2, 2, laminæ of the vertebræ; 3, 3, transverse processes; 4, 4, dorsal portions of the ribs; 5, 5, angles of the ribs.

Arising severally from the lower border of each rib and attached to the upper border of the rib below, are the eleven external intercostal muscles, the fibres of which have an oblique direction from above downward and forward. Attached to the inner borders of the ribs, are the internal intercostals, which have a direction from above downward and backward, nearly at right angles to the fibres of the external intercostals. There are also certain muscles attached to the thorax and spine, thorax and head, upper part of humerus, etc., which are capable of elevating either the entire chest or the ribs. These must act as muscles of inspiration when the attachments to the thorax become the movable points. Some of them are called into action during ordinary respiration; others act as auxiliaries when respiration is a little exaggerated, as after exercise, and are called ordinary auxiliaries; while others, which ordinarily have different uses, act only when respiration is difficult, and are called extraordinary auxiliaries.

The following are the principal muscles concerned in inspiration:

MUSCLES OF INSPIRATION.

*Ordinary Respiration.*

| MUSCLE. | ATTACHMENTS. |
|---|---|
| Diaphragm | Circumference of lower border of thorax. |
| Scalenus anticus | Transverse processes of third, fourth, fifth and sixth cervical vertebræ——tubercle of first rib. |
| Scalenus medius | Transverse processes of lower six cervical vertebræ——upper surface of first rib. |
| Scalenus posticus | Transverse processes of lower two or three cervical vertebræ——outer surface of second rib. |
| External intercostals | Outer borders of the ribs. |
| Sternal portion of internal intercostals | Borders of the costal cartilages. |
| Twelve levatores costarum | Transverse processes of dorsal vertebræ——ribs, between the tubercles and angles. |

*Ordinary Auxiliaries.*

| | |
|---|---|
| Serratus posticus superior | Ligamentum nuchæ, spinous processes of last cervical and upper two or three dorsal vertebræ——upper borders of second, third, fourth and fifth ribs, just beyond the angles. |
| Sterno-mastoideus | Upper part of sternum——mastoid process of temporal bone. |

*Extraordinary Auxiliaries.*

| | |
|---|---|
| Levator anguli scapulæ | Transverse processes of upper three or four cervical vertebræ——posterior border of superior angle of scapula. |
| Trapezius (superior portion) | Ligamentum nuchæ and seventh cervical vertebra——upper border of spine of scapula. |
| Pectoralis minor | Coracoid process of scapula——anterior surface and upper margins of third, fourth and fifth ribs, near the cartilages. |
| Pectoralis major (inferior portion) | Bicipital groove of humerus——costal cartilages and lower part of sternum. |
| Serratus magnus | Inner margin of posterior border of scapula——external surface and upper border of upper eight ribs. |

FIG. 46.—*Diaphragm* (Sappey).

1, 2, 3, central tendon; 4, right pillar; 5, left pillar; 6, 7, processes between the pillars; 8, 8, openings for the splanchnic nerves; 9, fibrous arch passing over the psoas magnus; 10, fibrous arch passing over the quadratus lumborum; 11, muscular fibres arising from these two arches; 12, 12, muscular fibres arising from the lower six ribs; 13, fibres from the ensiform cartilage; 14, opening for the vena cava; 15, opening for the œsophagus; 16, opening for the aorta; 17, 17, part of the transversalis muscle; 18, 18, aponeurosis; 19, 19, quadratus lumborum; 20, 20, psoas magnus; 21, fourth lumbar vertebra.

*Action of the Diaphragm.*—The descriptive and general anatomy of the diaphragm gives a pretty correct idea of its uses in respiration. It arises from the border of the lower circumference of the thorax and mounts into the cavity of the chest, forming a vaulted arch, or dome, with its concavity toward the abdomen and its convexity toward the lungs. In the central portion, there is a tendon of considerable size and shaped something like the club on a playing-card, with middle, right and left leaflets. The remainder of the organ is composed of radiating fibres of striated muscular tissue. The œsophagus, aorta and inferior vena cava pass through the diaphragm from the thoracic to the abdominal cavity, by three openings.

FIG. 47.—*Action of the diaphragm in inspiration* (Hermann).

Vertical section through the second rib on the right side. The broken and dotted lines show the descent of the diaphragm.

The opening for the œsophagus is surrounded by muscular fibres, by which it is partially closed when the diaphragm contracts in inspiration, as the fibres simply surround the tube and none are attached to its walls.

The orifice for the aorta is bounded by the bone and aponeurosis posteriorly, and in front, by a fibrous band to which the muscular fibres are attached, so that their contraction has a tendency rather to increase than to diminish the caliber of the vessel.

The orifice for the vena cava is surrounded entirely by tendinous structure, and contraction of the diaphragm, although it might render the form of the orifice more nearly circular, can have no effect upon its size.

In ordinary respiration, the descent of the diaphragm and its approximation to a plane are the chief phenomena observed; but as there is some resistance to the depression of the central tendon, it is probable that there is also a slight elevation of the inferior ribs.

The phenomena referable to the abdomen which coincide with the descent of the diaphragm can easily be observed in the human subject. As the diaphragm is depressed, it necessarily pushes the viscera before it, and inspiration is therefore accompanied by protrusion of the abdomen. This may be rendered very marked by a forced or deep inspiration.

The effects of the action of the diaphragm upon the size of its orifices are chiefly limited to the œsophageal opening. The anatomy of the parts is such that contraction of the muscular fibres has a tendency to close this orifice. The contraction of the diaphragm is auxiliary to the action of the muscular walls of the œsophagus itself, by which the cardiac opening of the stomach is regularly closed during inspiration. This may become important when the stomach is much distended; for descent of the diaphragm compresses all the abdominal organs and might otherwise cause regurgitation of food.

The contractions of the diaphragm are animated almost exclusively, if not exclusively, by the phrenic nerve; a nerve which, having the office of supplying the most important respiratory muscle, derives its filaments from a number of sources. It arises from the third and fourth cervical nerves, receiving a branch from the fifth and sometimes from the sixth. It then passes through the chest, penetrates the diaphragm, and is distributed to its under surface. Stimulation of this nerve produces convulsive contractions of the diaphragm, and its section paralyzes the muscle almost completely.

From the great increase in the capacity of the chest produced by the action of the diaphragm and its constant and universal action in respiration, it must be regarded as by far the most important and efficient of the muscles of inspiration.

Hiccough, sobbing, laughing and crying are due mainly to the action of the diaphragm, particularly hiccough and sobbing, which are produced by spasmodic contractions of this muscle, generally not under the control of the will.

*Action of the Muscles which elevate the Ribs.—Scalene Muscles.*—In ordinary respiration, the ribs and the entire chest are elevated by the combined action of a number of muscles. The three scalene muscles are attached to the cervical vertebræ and the first and second ribs. These muscles, which act particularly upon the first rib, must elevate with it, in inspiration, the rest of the thorax. The articulation of the first rib with the vertebral column is very movable, but it is joined to the sternum by a very short cartilage, which allows of very little movement, so that its elevation necessarily carries with it the sternum. This movement increases both the transverse and antero-posterior diameters of the thorax, on account of the mode of articulation and direction of the ribs, which are somewhat rotated as well as rendered more horizontal.

*Intercostal Muscles.*—Concerning the mechanism of the action of these muscles there is considerable difference of opinion among physiologists; so much, indeed, that the question is still left in some uncertainty. The most extended researches on this point are those of Beau and Maissiat (1843), and Sibson (1846). The latter seem to settle the question of the mode of action of the intercostals and explain satisfactorily certain points which even now are not generally appreciated. Onimus, and more recently, Laborde, have shown, by experiments upon decapitated criminals, that the external intercostals raise and the internal intercostals depress the ribs, thus confirming the views of Sibson.

In the dorsal region, the spinal column forms an arch with its concavity looking toward the chest, and the ribs increase in length progressively, from above downward, to the deepest portion of the arch, where they are longest, and then become progressively shorter. "During inspiration the ribs approach to or recede from each other according to the part of the arch with which they articulate; the four superior ribs approach each other anteriorly and recede from each other posteriorly; the fourth and fifth ribs, and the intermediate set (sixth, seventh, and eighth), move further apart to a moderate, the diaphragmatic set (four inferior), to a great extent. The upper edge of each of these ribs glides toward the vertebræ in relation to the lower edge of the rib above, with the exception of the lowest rib which is stationary" (Sibson). These movements increase the antero-posterior and transverse diameters of the thorax. As the ribs are elevated and become more nearly horizontal, they must push forward the lower portion of the sternum. Their configuration and mode of articulation with the vertebræ are such that they can not be elevated without undergoing a considerable rotation, by which the concavity looking directly toward the lungs is increased, and with it the lateral diameter of the chest. All the intercostal spaces posteriorly are widened in inspiration.

FIG. 48.—*Elevation of the ribs in inspiration* (Béclard).
The dark lines represent the ribs, sternum and costal cartilages in inspiration.

The ribs are elevated by the action of the external intercostals, the sternal portion of the internal intercostals and the levatores costarum. The external intercostals are situated between the ribs only, and are wanting in the region of the costal cartilages. As the vertebral extremities of the ribs are the pivots on which these levers move, and as the sternal extremities are movable, the direction of the fibres of the intercostals from above downward and forward renders elevation of the ribs a necessity of their contraction, if it can be assumed that the first rib is fixed or at least does not move downward. The scalene muscles elevate the first rib in ordinary inspiration; and in deep inspiration, this takes place to such an extent as to palpably carry with it the sternum and the lower ribs. Theoretically, then, the external intercostals can do nothing but render the ribs more nearly horizontal.

If the external intercostals be exposed in the dog—in which the costal type of respiration is very marked—close observation can hardly fail to show that these muscles enter into action in inspiration. If attention be directed to the sternal portion of the internal intercostals, situated between the costal cartilages, their fibres having a direction from above downward and backward, it is equally evident that they enter into action with inspiration. By artificially inflating the lungs after death, it is seen that when the lungs are filled with air, the fibres of these muscles are shortened (Sibson). In inspiration the ribs are all separated posteriorly; but laterally and anteriorly, some are separated (all below the fourth), and some are approximated (all above the fourth). Thus all the interspaces, except the anterior portion of the upper three, are widened in inspiration. Sibson has shown by inflation of the chest, that although the ribs are separated from each other, the attachments of the intercostals are approximated. The ribs, from an oblique position, are rendered nearly horizontal; and consequently the inferior attachments of the intercostals are brought nearer the spinal column, while the superior attachments to the upper borders of the ribs are slightly removed from it. Thus these muscles are shortened. If, by separating and elevating the ribs, the muscles be shortened, it follows that shortening of the muscles will necessarily elevate and separate the ribs. In the three superior interspaces, the constant direction of the ribs is nearly horizontal, and the course of the intercostal fibres is not so oblique as in those situated between the lower ribs. These spaces are narrowed in inspiration. The muscles between the costal cartilages have a direction opposite to that of the external intercostals and act upon the ribs from the sternum, as the others do from the spinal column. The superior interspace is narrowed, and the others are widened in inspiration.

*Levatores Costarum.*—The action of these muscles can not be mistaken. They have immovable points of origin, the transverse processes of twelve vertebræ from the last cervical to the eleventh dorsal, and spreading out like a fan, are attached to the upper edges of the ribs between the tubercles and the angles. In inspiration they contract and assist in the elevation of the ribs.

*Auxiliary Muscles of Inspiration.*—The muscles which have just been considered are competent to increase the capacity of the thorax sufficiently in ordinary respiration; but there are certain muscles attached to the chest and the upper part of the spinal column or the upper extremities, which may act in inspiration, although ordinarily the chest is the fixed point and they move the head, neck or arms. These muscles are brought into action when the movements of respiration are exaggerated. When this exaggeration is but slight and is physiological, as after exercise, certain of the ordinary auxiliaries act for a time, until the tranquillity of the movements is restored; but when there is obstruction in the respiratory passages or when respiration is difficult from any cause, threatening suffocation, all the muscles which can by any possibility raise the chest are brought into action. These are put down in the table under the head of extraordinary auxiliaries. Most of these muscles can voluntarily be brought into play to raise the chest, and the mechanism of their action can in this way be demonstrated.

*Serratus Posticus Superior.*—This muscle, by reversing its ordinary action, is capable of increasing the capacity of the thorax.

*Sterno-mastoideus.*—That portion of the muscle which is attached to the mastoid process of the temporal bone and the sternum, when the head is fixed, is capable of acting as a muscle of inspiration. It does not act in ordinary respiration, but its contractions can be readily observed whenever respiration is hurried or exaggerated.

The following muscles as a rule act as muscles of inspiration only when respiration is very difficult or labored:

*Levator Anguli Scapulæ and Superior Portion of the Trapezius.*—Movements of the scapula have often been observed in labored respiration. Its elevation during inspiration is effected chiefly by the levator anguli scapulæ and the upper portion of the trapezius.

*Pectoralis Minor and Inferior Portion of the Pectoralis Major.*—These muscles act together to raise the ribs in difficult respiration. The pectoralis minor is the more efficient. With the coracoid process as the fixed point, this muscle is capable of powerfully assisting in the elevation of the ribs. That portion of the pectoralis major which is attached to the lower part of the sternum and costal cartilages is capable of acting from its insertion into the bicipital groove of the humerus, when the shoulders are fixed, in concert with the pectoralis minor.

*Serratus Magnus.*—Acting from the scapula as the fixed point, this muscle is capable of assisting the pectorals in raising the ribs and becomes a powerful auxiliary in difficult inspiration.

The uses of the principal inspiratory muscles have been considered without taking up those which have an insignificant or undetermined action. In many animals, the nares are considerably distended in inspiration; and in the horse, which does not respire by the mouth, these movements are as essential to life as are the respiratory movements of the larynx. In man, as a rule the nares undergo no movements unless respiration be somewhat exaggerated. In very difficult respiration the mouth is opened at each inspiratory act.

The division into muscles of ordinary inspiration, ordinary auxiliaries and extraordinary auxiliaries, must not be taken as absolute. In the male, in ordinary respiration, the diaphragm, intercostals and levatores costarum are the principal inspiratory muscles, and the action of the scaleni, with the consequent elevation of the sternum, is commonly very slight or it may be wanting. In the female the movements of the upper parts of the chest are more marked, and the scaleni, the serratus posticus superior, and sometimes the sterno-mastoid, are brought into action in ordinary respiration. In the different types of respiration, the action of the muscles engaged in ordinary respiration necessarily presents considerable variations.

*Expiration.*—The air is expelled from the lungs, in ordinary expiration, by a simple and comparatively passive process. The lungs contain a large number of elastic fibres surrounding the air-cells and the smallest ramifications of the bronchial tubes, which give them great elasticity. The thoracic walls are also very elastic, particularly in young persons. After the muscles which increase the capacity of the thorax cease their action, the elasticity of the costal cartilages and the tonicity of the muscles which have been put on the stretch restore the chest to what may be called its passive dimensions. This elasticity is likewise capable of acting as an inspiratory force when the chest has been compressed in any way. There are also certain muscles, the action of which is to draw the ribs downward and which, in tranquil respiration, are antagonistic to those which elevate the ribs. Aside from this, many operations, such as speaking, blowing, singing etc., require powerful, prolonged or complicated acts of expiration, in which many muscles are brought into play.

Expiration may be considered as depending upon two causes:

1. The passive influence of the elasticity of the lungs and thoracic walls.

2. The action of certain muscles, which either diminish the transverse and antero-posterior diameters of the chest by depressing the ribs and sternum, or the vertical diameter, by pressing up the abdominal viscera against the diaphragm.

*Influence of the Elasticity of the Pulmonary Structure and Walls of the Chest.*—It is easy to understand the influence of the elasticity of the pulmonary structure in expiration. From the collapse of the lungs when openings are made in the chest, it is seen that even after the most complete expiration, these organs have a tendency to expel part of their gaseous contents, which can not be fully satisfied until the chest is opened. They remain partially distended, on account of the impossibility of collapse of the thoracic walls beyond a certain point; and by virtue of their elasticity, they exert a suction force upon the diaphragm, causing it to form a vaulted arch, or dome above the level of the lower circumference of the chest. When the lungs are collapsed, the diaphragm hangs loosely between the abdominal and thoracic cavities. In inspiration and in expiration, then, the relations between the lungs and diaphragm are reversed. In inspiration, the descending diaphragm exerts a suction force on the lungs, drawing them downward; in expiration, the elastic lungs exert a suction force upon the diaphragm, drawing it upward. This antagonism is one of the causes of the great power and importance of the diaphragm as an inspiratory muscle.

The elasticity of the lungs operates chiefly upon the diaphragm in reducing the capacity of the chest; for the walls of the thorax, by reason of their own elasticity, have a reaction which succeeds the movements produced by the inspiratory muscles. Although this is the main action of the lungs themselves in expiration, their relations to the walls of the thorax are important. By virtue of their elasticity, they assist the passive collapse of the chest. When they lose this property to any considerable extent, as in vesicular emphysema, they offer a notable resistance to the contraction of the thorax; so much indeed, that in old cases of this disease the thoracic movements are restricted, and the chest presents a characteristic rounded and distended appearance.

Little more need be said concerning the passive movements of the thoracic walls. When the action of the inspiratory muscle ceases, the ribs regain their oblique direction, the intercostal spaces are narrowed, and the sternum, if it have been elevated and drawn forward, falls back to its place, simply by virtue of the elasticity of the parts.

*Action of Muscles in Expiration.*—The following are the principal muscles concerned in expiration:

MUSCLES OF EXPIRATION.

*Ordinary Respiration.*

| MUSCLE. | ATTACHMENTS. |
|---|---|
| Osseous portion of internal intercostals.. | Inner borders of the ribs. |
| Infracostales.............................. | Inner surfaces of the ribs. |
| Triangularis sterni....................... | Ensiform cartilage, lower borders of sternum, lower three or four costal cartilages——cartilages of the second, third, fourth and fifth ribs. |
| *Auxiliaries.* | |
| Obliquus externus....................... | External surface and inferior borders of eight inferior ribs——anterior half of the crest of the ileum, Poupart's ligament, linea alba. |
| Obliquus internus........................ | Outer half of Poupart's ligament, anterior two-thirds of the crest of the ileum, lumbar fascia ——cartilages of four inferior ribs, linea alba, crest of the pubis, pectineal line. |
| Transversalis.............................. | Outer third of Poupart's ligament, anterior two-thirds of the crest of the ileum, lumbar vertebræ, inner surface of cartilages of six inferior ribs——crest of the pubis, pectineal line, linea alba. |
| Sacro-lumbalis........................... | Sacrum——angles of six inferior ribs. |

*Internal Intercostals.*—The internal intercostals have different uses in different parts of the thorax. They are attached to the inner borders of the ribs and costal cartilages. Between the ribs they are covered by the external intercostals, but between the costal cartilages they are covered simply by aponeurosis. Their direction is from above downward and backward, nearly at right angles to the external intercostals. The action of that portion of the internal intercostals situated between the costal cartilages has already been noted. They assist the external intercostals in elevating the ribs in inspiration. Between the ribs these muscles are directly antagonistic to the external intercostals. They are more nearly at right angles to the ribs, particularly in that portion of the thorax where the obliquity of the ribs is greatest. They are elongated when the chest is distended, and are shortened when the chest is collapsed (Sibson). This fact, taken in connection with experiments on living animals, shows that they are muscles of expiration. Theiı contraction tends to depress the ribs and consequently to diminish the capacity of the chest.

*Infracostales.*—These muscles, situated at the posterior part of the thorax, are variable in size and number. They are most common at the lower part of the chest. Their fibres arise from the inner surface of one rib to be inserted into the inner surface of the first, second or third rib below. The fibres follow the direction of the internal intercostals, and acting from their lower attachments, their contractions assist these muscles in drawing the ribs downward.

*Triangularis Sterni.*—There has never been any doubt concerning the expiratory action of the triangularis sterni. From its origin, the ensiform cartilage, lower borders of the sternum, and lower three or four costal cartilages, it acts upon the cartilages of the second, third, fourth and fifth ribs, to which it is attached, drawing them downward and thus diminishing the capacity of the chest.

The above-mentioned muscles are called into action in ordinary, tranquil respiration, and their sole office is to diminish the capacity of the chest. In labored or difficult expiration, and in the acts of blowing, phonation etc., other muscles, which are called auxiliaries, play a more or less important part. These muscles all enter into the formation of the walls of the abdomen, and their general action in expiration is to press the abdominal viscera and diaphragm into the thorax and diminish its vertical diameter. Their action is voluntary; and by an effort of the will, it may be opposed more or less by the diaphragm, by which means the duration or extent of the expiratory act is regulated. They are also attached to the ribs or costal cartilages, and while they press the diaphragm upward, they depress the ribs and thus diminish the antero-posterior and transverse diameters of the chest. In this action, they may be opposed by the voluntary contraction of the muscles which raise the ribs, also for the purpose of regulating the force of the expiratory act.

In labored respiration in disease and in the hurried respiration which follows violent exercise, the auxiliary muscles of expiration, as well as of inspiration, are called into action to a considerable extent.

*Obliquus Externus.*—This muscle, in connection with the obliquus internus and transversalis, is efficient in foreed or labored expiration, by pressing the abdominal viscera against the diaphragm. Acting from its attachments to the linea alba, the crest of the ileum and Poupart's ligament, by its attachment to the eight inferior ribs, it draws the ribs downward.

*Obliquus Internus.*—This muscle also acts in forced expiration, by compressing the abdominal viscera. The direction of its fibres is from below upward and forward. Acting from its attachments to the crest of the ileum, Poupart's ligament and the lumbar fascia, by its attachments to the cartilages of the four inferior ribs, it draws them downward. The direction of the fibres of this muscle is the same as that of the internal intercostals. By its action the ribs are drawn inward as well as downward.

*Transversalis.*—The expiratory action of this muscle is mainly in compressing the abdominal viscera.

*Sacro-lumbalis.*—This muscle is situated at the posterior portion of the abdomen and thorax. Its fibres pass from its origin at the sacrum, upward and a little outward, to be inserted into the six inferior ribs at their angles. In expiration it draws the ribs downward, acting as an antagonist to the lower levatores costarum.

There are some other muscles which may be used in forced expiration, assisting in the depression of the ribs, such as the serratus posticus inferior, the superior fibres of the serratus magnus and the inferior portion of the trapezius, but their action in respiration is unimportant.

*Types of Respiration.*—In the movements of expansion of the chest, although all the muscles which have been classed as ordinary inspiratory muscles are brought into action to a greater or less extent, the fact that certain sets may act in a more marked manner than others has led physiologists to recognize different types of respiration. Three types are generally given in works on physiology:

1. *The Abdominal Type.*—In this, the action of the diaphragm and the consequent movements of the abdomen are most prominent.

2. *The Inferior Costal Type.*—In this, the action of the muscles which expand the lower part of the thorax, from the seventh rib inclusive, is most prominent.

3. *The Superior Costal Type.*—In this, the action of the muscles which dilate the thorax above the seventh rib and which elevate the entire chest is most prominent.

The abdominal type is most marked in children less than three years of age, irrespective of sex, respiration being carried on almost exclusively by the diaphragm.

At a variable period after birth, a difference in the types of respiration in the sexes is observed. In the male the abdominal conjoined with the inferior costal type is predominant, and this continues through life. In the female the inferior costal type is insignificant and the superior costal type predominates. Without discussing the question as to the exact age when this difference in the sexes first makes its appearance, it may be stated in general terms, that a short time before the age of puberty in the female, the superior costal type becomes more marked and soon predominates. In the male, respiration continues to be carried on mainly by the diaphragm and the lower part of the chest.

The cause of the pronounced movements of the upper part of the chest in the female has been the subject of considerable discussion. It is probably due, in a great measure, to the mode of dress now so general in civilized countries, which confines the lower part of the chest and renders movements of expansion somewhat difficult. In a series of observations by Thomas J. Mays (1887), upon eighty-two chests of Indian girls at the Lincoln Institution in

Philadelphia, between ten and twenty years of age, who had never worn tight clothing, the abdominal type of respiration was found to predominate, the respiratory tracings hardly differing from the tracings in the male. These observations seem to show, in opposition to the views of Hutchinson and others, that the predominance of the superior costal type in the female is confined to civilized races; but it is certain that females accommodate themselves more readily than the male to the superior costal type; and this is probably a provision against the physiological enlargement of the uterus in pregnancy, which nearly arrests all respiratory movements except those of the upper part of the chest. In pathology it is observed that females are able to carry, without great inconvenience, a large quantity of water in the abdominal cavity; while a much smaller quantity, in the male, produces great distress from difficulty of breathing.

*Frequency of the Respiratory Movements.*—In counting the respiratory acts, it is desirable that the subject be unconscious of the observation, otherwise their normal rhythm is likely to be disturbed. Of all who have written on this subject, Hutchinson has presented the largest and most reliable collection of facts. This observer ascertained the number of respiratory acts per minute, in the sitting posture, in 1,897 males. The results of his observations, with reference to frequency, are given in the following table:

| RESPIRATIONS PER MINUTE. | NUMBER OF CASES. |
|---|---|
| 9 to 16 | 79 |
| 16 | 239 |
| 17 | 105 |
| 18 | 195 |
| 19 | 74 |
| 20 | 561 |
| 21 | 129 |
| 22 | 143 |
| 23 | 42 |
| 24 | 243 |
| 24 to 40 | 87 |

Although this table shows considerable variation in different individuals, the great majority (1,731) breathed sixteen to twenty-four times per minute. Nearly a third breathed twenty times per minute, a number which may be taken as the average.

The relations of the respiratory acts to the pulse are quite constant in health. It has been shown by Hutchinson that the proportion in the great majority of instances is one respiratory act to four pulsations of the heart. The same proportion generally obtains when the pulse is accelerated in disease, except when the pulmonary organs are involved.

Age has an influence on the frequency of the respiratory acts, corresponding with what has already been noted with regard to the pulsations of the heart.

The following are the results of observations on 300 males (Quetelet):

44 respirations per minute, soon after birth;

26, at the age of five years;
20, between fifteen and twenty years;
19, between twenty and twenty-five years;
16, about the thirtieth year;
18, between thirty and fifty years.

The influence of sex is not marked in very young children. There is no difference between males and females at birth; but in young women, the respirations are a little less frequent than in young men of the same age.

The various physiological conditions which have been noted as affecting the pulse have a corresponding influence on respiration. In sleep the number of respiratory acts is diminished by about twenty per cent. (Quetelet). Muscular effort accelerates the respiratory movements *pari passu* with the movements of the heart.

*Relations of Inspiration and Expiration to each other—Respiratory Sounds.*—In ordinary respiration, inspiration is produced by the action of muscles, and expiration, by the passive reaction of the lungs and of the elastic walls of the thorax. The inspiratory and expiratory acts do not immediately follow each other. Beginning with inspiration, it is found that this act maintains about the same intensity throughout. There is then a very brief interval, when expiration follows, which has its maximum of intensity at the beginning of the act and gradually dies away. Between the acts of expiration and inspiration is an interval, which is somewhat longer than the interval between inspiration and expiration.

The duration of expiration is generally somewhat longer than that of inspiration, although the two acts may be nearly, or in some instances, quite equal. After five to eight ordinary respiratory acts, an effort generally occurs which is rather more profound than usual, by which the air in the lungs is more thoroughly changed. The temporary arrest of the acts of respiration in violent muscular efforts, in straining, in parturition etc., is sufficiently familiar.

Ordinarily respiration is not accompanied by any sound which can be heard without applying the ear directly, or by the intervention of a stethoscope, to the chest, except when the mouth is closed and breathing is carried on exclusively through the nasal passages, when a soft, breezy sound accompanies both acts. If the mouth be opened sufficiently to admit the free passage of air, no sound is to be heard in health. In sleep the respirations are more profound; and if the mouth be closed the sound is rather more intense.

Snoring, which sometimes accompanies the respiratory acts during sleep, occurs when the air passes through both the mouth and the nose. It is more marked in inspiration, sometimes accompanying both acts, and sometimes it is not heard in expiration. It is not necessary to describe the characters of a sound so familiar. Snoring is an idiosyncrasy in many individuals, although those who do not snore habitually may do so when the system is unusually exhausted and relaxed. It occurs only when the mouth is open, and the sound is produced by vibration and a sort of flapping of the velum pendulum palati, between the two currents of air from the mouth and nose, together with a vibration in the column of air itself.

Applying the stethoscope over the larynx or trachea, a sound is heard, of a distinctly and purely tubular character, accompanying both acts of respiration. In inspiration, according to the late Dr. Austin Flint, "it attains its maximum of intensity quickly after the development of the sound and maintains the same intensity to the close of the act, when the sound abruptly ends, as if suddenly cut off." After a brief interval, the sound of expiration follows. This is also tubular in quality. It soon attains its maximum of intensity, but unlike the sound of inspiration, it gradually dies away and is lost imperceptibly. It is seen that these phenomena correspond with the nature of the two acts of respiration.

Sounds approximating in character to the foregoing are heard over the bronchial tubes before they penetrate the lungs.

Over the substance of the lungs, a sound may be heard entirely different in its character from that heard over the larynx, trachea or bronchial tubes. In inspiration the sound is much less intense than over the trachea and has a breezy, expansive, or what is called in auscultation, a vesicular character. It is much lower in pitch than the tracheal sound. It is continuous and rather increases in intensity from its beginning to its termination, ending abruptly, like the tracheal inspiratory sound. The sound is produced in part by the movement of air in the small bronchial tubes, but chiefly by the expansion of the air-cells of the lungs. It is followed, without an interval, by the sound of expiration, which is shorter—one-fifth or one-fourth as long—lower in pitch and much less intense. A sound is not always heard in expiration.

The variations in the intensity of the respiratory sounds in different individuals are very considerable. As a rule they are more intense in young persons; which has given rise to the term puerile respiration, when the sounds are exaggerated in parts of the lung, in certain cases of disease. The sounds are generally more intense in females than in males, particularly in the upper regions of the thorax.

It is difficult by any description or comparison to convey an accurate idea of the character of the sounds heard over the lungs and air-passages, and it is unnecessary to make the attempt, when they can be so easily studied in the living subject.

*Coughing, Sneezing, Sighing, Yawning, Laughing, Sobbing and Hiccough.*—These peculiar acts demand a few words of explanation. Coughing and sneezing are generally involuntary acts, produced by irritation in the air-tubes or nasal passages, although coughing is often voluntary. In both of these acts, there is first a deep inspiration followed by a convulsive action of the expiratory muscles, by which the air is violently expelled with a characteristic sound, in the one case by the mouth, and in the other by the mouth and nares. Foreign bodies lodged in the air-passages are frequently expelled in violent fits of coughing. In hypersecretion of the bronchial mucous membrane, the accumulated mucus is carried by the act of coughing either to the mouth or well into the larynx, when it may be expelled by the act of exspuition. When either of these acts is the result of irritation from a foreign substance or from secretions, it may be modified or partly smothered by the will, but is not completely under control. The sensibility of the mucous membrane at the summit of the air-passages usually protects them from the entrance of foreign matters, both liquid and solid; for the slightest impression received by the membrane gives rise to a violent and involuntary cough, by which the offending substance is removed. The glottis, also, is spasmodically contracted.

In sighing, a prolonged and deep inspiration is followed by a rapid and generally an audible expiration. This occurs, as a general rule, once in five to eight respiratory acts, for the purpose of changing the air in the lungs more completely, and it is due to an exaggeration of the cause which gives rise to the ordinary acts of respiration. When due to depressing emotions, it has the same cause; for at such times respiration is less efficiently performed. Yawning is an analogous process, but it differs from sighing in the fact that it is involuntary and can not be produced by an effort of the will. It is characterized by a wide opening of the mouth and a very profound inspiration. Yawning is generally assumed to be an evidence of fatigue, but it often occurs from a sort of contagion. When not the result of imitation, it has the same exciting cause as sighing—deficient oxygenation of the blood—and it is followed by a sense of satisfaction, which shows that it meets some decided want on the part of the system.

Laughing and sobbing, although expressing opposite conditions, are produced by very nearly the same action. The characteristic sounds accompanying these acts are the result of short, rapid and convulsive movements of the diaphragm, attended with contractions of the muscles of the face, which produce the expressions characteristic of hilarity or grief. Although to a certain extent under the control of the will, these acts are mainly involuntary. Violent and convulsive laughter may be excited in many individuals by titillation of certain portions of the surface of the body. Laughter and sometimes sobbing, like yawning, may be the result of involuntary imitation.

Hiccough is a peculiar modification of the act of inspiration, to which it is exclusively confined. It is produced by a sudden, convulsive and entirely involuntary contraction of the diaphragm, accompanied by a spasmodic constriction of the glottis. The contraction of the diaphragm is more extensive than in laughing and sobbing and occurs only once every four or five respiratory acts.

### Capacity of the Lungs, and the Quantity of Air changed in the Respiratory Acts.

The volume of air ordinarily contained in the lungs is about two hundred cubic inches (3,277 c.c.); but it is evident, from the simple experiment of opening the chest, when the elastic lungs collapse and expel a certain quantity of air which can not be removed while the lungs are *in situ*, that a part of the gaseous contents of these organs necessarily remains after the most complete and forcible expiration. After an ordinary act there is a certain quantity of air in the lungs which can be expelled by a forced expiration. In ordinary respiration a comparatively small volume of air is introduced with inspiration, and a nearly equal quantity is expelled by the succeeding expiration. By the extreme action of all the inspiratory muscles in a forced inspiration, a supplemental quantity of air may be introduced into the lungs, which then contain much more than they ever do in ordinary respiration. For convenience of description, physiologists have adopted the following names, which are applied to these various volumes of air:

1. *Residual Air;* that which is not and can not be expelled by a forced expiration.

2. *Reserve Air;* that which remains after an ordinary expiration, deducting the residual air.

3. *Tidal, or Ordinary Breathing Air;* that which is changed by the ordinary acts of inspiration and expiration.

4. *Complemental Air;* the excess over the ordinary breathing air, which may be introduced by a forcible inspiration.

In measuring the air changed in ordinary breathing, it has been found that the acts of respiration are so easily influenced and it is so difficult to experiment on any individual without his knowledge, that the results of many good observers are not to be relied upon. This is one of the most important of the questions under consideration. The difficulties in the way of estimating with accuracy the residual, reserve or complemental volumes, will readily suggest themselves. The observations on these points which may be taken as the most definite and exact are those of Herbst and of Hutchinson. Those of the last-named observer are very elaborate and were made on a large number of subjects of both sexes and of all ages and occupations. They are generally accepted by physiologists, as the most extended and accurate.

*Residual Air.*—Perhaps there is not one of the questions under consideration more difficult to answer definitely than that of the quantity of air which remains in the lungs after a forced expiration; but it fortunately is not one of any great practical importance. The residual air remains in the lungs as a physical necessity. The lungs in health are always in contact with the walls of the thorax; and when this cavity is reduced to its smallest dimensions, it is impossible that any more air should be expelled. The volume which thus remains has been variously estimated. The residual volume has been estimated at about one hundred cubic inches (1,639 c.c.), but the quantity varies very considerably in different individuals (Hutchinson). Taking everything into consideration, it may be assumed that this estimate is as nearly correct as any.

*Reserve Air.*—This name is given to the volume of air which may be expelled and changed by a voluntary effort, but which remains in the lungs, added to the residual air, after an ordinary act of expiration. It may be estimated, without any reference to the residual air, by forcibly expelling air from the lungs, after an ordinary expiration. The average volume, according to Hutchinson, is one hundred cubic inches (1,639 c.c.).

More or less of the reserve air is changed whenever there is a necessity for a more complete renovation of the contents of the lungs than ordinary. It is encroached upon in the unusually profound inspiration and expiration which occur once in every five to eight acts. It is used in certain prolonged vocal efforts, in blowing etc. Added to the residual air, it constitutes the minimum capacity of the lungs in ordinary respiration. As it is continually receiving watery vapor and carbon dioxide, it is always more or less vitiated, and when reënforced by the breathing air, which enters with inspiration, is continually in circulation, in obedience to the law of the diffusion of gases. Those who are in the habit of arresting respiration for a time, learn to change the reserve air as completely as possible by several forcible acts and then fill the lungs with fresh air. In this way they are enabled to suspend the respiratory acts for two or three minutes without inconvenience. The introduction of fresh air with each inspiration, and the constant diffusion which is going on and by which the proper quantity of oxygen finds its way to the air-cells, give, in ordinary breathing, a composition to the air in the deepest portions of the lungs which insures a constant aëration of the blood.

*Tidal, or Ordinary Breathing Air.*—The volume of air which is changed in the ordinary acts of respiration is subject to certain physiological variations; and the respiratory movements, as regards their extent, are so easily influenced, that great care is necessary to avoid error in estimating the volume of ordinary breathing air. As a mean of the results obtained by Herbst and by Hutchinson, the average volume of breathing air, in a man of ordinary stature, is twenty cubic inches (327·7 c.c.). According to Hutchinson, in perfect repose, when the respiratory movements are hardly perceptible, not more than seven to twelve cubic inches (114·7 to 196·6 c.c.) are changed; while, under excitement, the volume may be increased to seventy-seven cubic inches (1,261·8 c.c.). The breathing volume progressively increases in proportion to the stature of the individual, and bears no definite relation to the apparent capacity of the chest (Herbst).

*Complemental Air.*—The thorax may be so enlarged by an extreme voluntary inspiratory effort as to contain a quantity of air much larger than after an ordinary inspiration. The additional volume of air thus taken in may be estimated by measuring all the air which can be expelled from the lungs after the most profound inspiration, and deducting the sum of the reserve air and breathing air. This quantity has been found by Hutchinson to vary in different individuals, bearing a close relation to stature. The mean complemental volume is one hundred and ten cubic inches (1,802·9 c. c.).

The complemental air is drawn upon whenever an effort is made which requires a temporary arrest of respiration. Brief and violent muscular exertion is generally preceded by a profound inspiration. In sleep, as the volume of breathing air is somewhat increased, the complemental air is encroached upon. A part or the whole of the complemental air is also used in certain vocal efforts, in blowing, in yawning, in the deep inspiration which precedes sneezing, in straining etc.

*Extreme Breathing Capacity.*—By the extreme breathing capacity is meant the volume of air which can be expelled from the lungs by the most forcible expiration after the most profound inspiration. This has been called by Hutchinson, the vital capacity, as signifying "the volume of air which can be displaced by living movements." Its volume is equal to the sum of the reserve air, the breathing air and the complemental air, and it represents the extreme capacity of the chest, less the residual air. Its physiological importance is due to the fact that it can readily be determined by an appropriate apparatus, the spirometer, and comparisons can thus be made between different individuals, both healthy and diseased. The number of observations on this point made by Hutchinson amounts in all to a little less than five thousand.

The extreme breathing capacity in health is subject to variations which have been shown to bear a very close relation to the stature of the individual. Hutchinson begins with the proposition that in a man of medium height (five feet eight inches, or 170·2 centimetres), it is equal to two hundred and thirty cubic inches (3,768·6 c. c.).

The most striking result of the experiments of Hutchinson, with regard to the modifications of the vital capacity, is that it bears a definite relation to stature, without being affected in a very marked degree by weight or by the circumference of the chest. This is especially remarkable, as it is well known that height does not depend so much upon the length of the body as upon the length of the lower extremities. He ascertained that for every inch ($\frac{1}{4}$ centimetre) in height, between five and six feet (152·4 and 182·9 centimetres), the extreme breathing capacity is increased by eight cubic inches (131·1 c. c.).

Age has an influence, though less marked than stature, upon the extreme breathing capacity. As the result of 4,800 observations on males, it was ascertained that the volume increases with age up to the thirtieth year, and progressively decreases, with tolerable regularity, from the thirtieth to the sixtieth year. These figures, though necessarily subject to certain individual variations, may be taken as a basis for examinations of the extreme breathing capacity in disease.

*Relations in Volume of the Expired to the Inspired Air.*—A certain proportion of the inspired air is lost in respiration, so that the air expired is always a little less in volume than that which is taken into the lungs. The loss was put by Davy at $\frac{1}{70}$, and by Cuvier at $\frac{1}{60}$ of the volume of air introduced. Observations on this point, to be exact, must include a considerable number of respiratory acts; and from the difficulty of continuing respiration in a perfectly regular and normal manner when the attention is directed to the respiratory movements, the most accurate results may probably be obtained from experiments on the lower animals. Despretz caused six young rabbits to respire for two hours in a confined space containing 2,990 cubic inches (49,000 c. c.) of air, and ascertained that the volume had diminished by sixty-one cubic inches (1,000 c. c.), or a little more than one-fiftieth. Adopting the approximations of Davy and Cuvier, applied to the human subject, as nearly correct, it may be assumed that in the lungs, $\frac{1}{70}$ to $\frac{1}{50}$ of the inspired air is lost.

*Diffusion of Air in the Lungs.*—When it is remembered that with each inspiration, but about twenty cubic inches (327·7 c. c.) of fresh air are introduced, sufficient only to fill the trachea and larger bronchial tubes, it is evident that some forces must act by which this fresh air finds its way into the air-cells, and the vitiated air is brought into the larger tubes, to be expelled with the succeeding expiration.

The interchange between the fresh air in the upper portions of the respiratory apparatus and the air in the deeper parts of the lungs is constantly going on by simple diffusion aided by the active currents or impulses produced by the alternate movements of the chest. In the respiratory apparatus, at the end of an inspiration, the atmospheric air, composed of a mixture of oxygen and nitrogen, is introduced into the tubes with a considerable impetus and is brought into contact with the gas in the lungs, which is heavier, as it contains a certain quantity of carbon dioxide. Diffusion then takes place, aided by the elastic lungs, which are gradually forcing the gaseous contents out of the cells, until a certain portion of the air loaded with carbon dioxide finds its way to the larger tubes, to be thrown off in expiration, its place being supplied by the fresh air.

In obedience to the law established by Graham, that the diffusibility of gases is inversely proportionate to the square root of their densities, the penetration of atmospheric air, which is the lighter gas, to the deep portions of the lungs would take place with greater rapidity than the ascent of the air charged with carbon dioxide; so that eighty-one parts of carbon dioxide should be replaced by ninety-five parts of oxygen. It is found, indeed, that the volume of carbon dioxide exhaled is always less than the volume of oxygen absorbed. This diffusion is constantly going on, so that the air in the pulmonary vesicles, where the interchange of gases with the blood takes place, maintains a nearly uniform composition. The process of aëration of the blood, therefore, has little of that intermittent character which attends the muscular movements of respiration, which would occur if the entire gaseous contents of the lungs were changed with each respiratory act.

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## CHAPTER V.

### *CHANGES WHICH THE AIR AND THE BLOOD UNDERGO IN RESPIRATION.*

**Composition of the air—Consumption of oxygen—Exhalation of carbon dioxide—Relations between the quantity of oxygen consumed and the quantity of carbon dioxide exhaled—Sources of carbon dioxide in the expired air—Exhalation of watery vapor—Exhalation of ammonia—Exhalation of organic matter—Exhalation of nitrogen—Changes of the blood in respiration (hæmatosis)—Difference in color between arterial and venous blood—Comparison of the gases in venous and arterial blood—Analysis of the blood for gases—Nitrogen of the blood—Condition of the gases in the blood—Relations of respiration to nutrition etc.—The respiratory sense—Sense of suffocation—Respiratory efforts before birth—Cutaneous respiration—Breathing in a confined space—Asphyxia.**

FROM the allusions already made to the general process of respiration, it is apparent that before the discovery of the nature of the gases which compose the air and those which are exhaled from the lungs, it was impossible for physiologists to have any correct ideas of the nature of this important function. It is also evident that no definite knowledge of the processes of respiration could exist prior to the discovery of the circulation of the blood.

The discovery of the properties of oxygen and carbon dioxide were simply isolated facts and failed to develop any definite idea of the changes of the air and blood in respiration. The application of these facts was made by Lavoisier, whose observations mark the beginning of an accurate knowledge of the physiology of respiration. With the balance, Lavoisier showed the nature of the oxides of the metals; he discovered that carbon dioxide is formed by a union of carbon and oxygen; and noting the consumption of oxygen and the production of carbon dioxide in respiration, he advanced, for the first time, the view that the one was concerned in the production of the other. Although, as would naturally be expected, the doctrines of Lavoisier have been modified with the advances in science, he developed facts which have served as the starting-point of definite knowledge on this subject.

*Composition of the Air.*—Pure atmospheric air is a mechanical mixture of 79·19 parts of nitrogen with 20·81 parts of oxygen (Dumas and Boussingault). It contains, in addition, a very small quantity of carbon dioxide, about one part in two thousand. The air is never free from moisture, which is very variable in quantity, being generally more abundant at a high than at a low temperature. Floating in the atmosphere, are large numbers of minute organic bodies; and various odorous and other gaseous matters sometimes are present as accidental constituents.

In considering the processes of respiration, it is not necessary to take account of any of the constituents of the atmosphere except oxygen and nitrogen, the others being either inconstant or existing in excessively minute quantity. It is necessary to the regular performance of respiration, that the air should contain about four parts of nitrogen to one of oxygen, and have about the density which exists on the general surface of the globe. When the density is very much increased, as in mines, respiration is more or less disturbed. By exposure to a rarefied atmosphere, as in the ascent of high mountains or in aërial voyages, respiration may be very seriously interfered with, from the fact that less oxygen than usual is presented to the respiratory surface and the reduced atmospheric pressure diminishes the capacity of the blood for retaining gases.

Magendie and Bernard, in experimenting on the minimum proportion of oxygen in the air which is capable of sustaining life, found that a rabbit, confined under a bell-glass, with an arrangement for removing the carbon dioxide and water exhaled, as fast as they were produced, died of asphyxia when the quantity of oxygen became reduced to between three and five per cent.

A few experiments are on record in which the human subject and the lower animals have been made to respire for a time pure oxygen. Allen and Pepys confined animals for twenty-four hours in an atmosphere of pure oxygen without any notable results; but these experiments do not show that it would be possible to respire unmixed oxygen indefinitely without inconvenience. As it exists in the air, oxygen is undoubtedly in the best condition for the permanent maintenance of the respiratory function. The blood seems to have a certain capacity for the absorption of oxygen, which is not materially increased when the pure gas is respired.

The only other gas which has the power of maintaining respiration, even for a time, is nitrogen monoxide. This is appropriated by the blood-corpuscles with great avidity, and for a time it produces an exaggeration of the vital processes, with delirium etc., which has given it the common name of the laughing gas; but this condition is followed by anæsthesia, and finally by asphyxia, probably because the gas has so strong an affinity for the blood-corpuscles as to remain to a certain extent fixed, interfering with the interchange of gases which is essential to life. Notwithstanding this, experimenters have confined with impunity rabbits and other animals in an atmosphere of nitrogen monoxide for a number of hours. In all cases they became asphyxiated, but in some instances they were restored on being brought again into the ordinary atmosphere.

Other gases which may be introduced into the lungs either produce asphyxia, negatively, from the fact that they are incapable of carrying on respiration, like hydrogen or nitrogen, or positively, by a poisonous effect on the system. The most important of the gases which act as poisons are carbon monoxide, hydrogen monosulphide and arsenious hydride. Carbon monoxide unites with the coloring matter of the red corpuscles, forming carbon-monoxide-hæmaglobine. This union is so stable that it paralyzes the corpuscles as oxygen-carriers and produces death by asphyxia. It is probable that carbon dioxide is not in itself poisonous. Regnault and Reiset exposed animals (dogs and rabbits) for many hours, to an atmosphere containing twenty-three per cent. of carbon dioxide artificially introduced, with between thirty and forty per cent. of oxygen, without any ill effects.

*Consumption of Oxygen.*—The determination of the quantity of oxygen which is removed from the air by the process of respiration is important; and on this point, there is an accumulated mass of observations which are comparatively unimportant from the fact that they were made before the means of analysis of the gases were as accurate as they now are. In the observations of Regnault and Reiset, animals were placed in a receiver filled with air, a measured quantity of oxygen was introduced as fast as it was consumed by respiration, and the carbon dioxide was constantly removed and carefully estimated. In most of the experiments, the confinement did not appear to interfere with the functions of the animal, which ate and drank in the apparatus and was in as good condition at the termination as at the beginning of the observation. This method is much more accurate than that of simply causing an animal to breathe in a confined space, when the consumption of oxygen and accumulation of carbon dioxide and other matters must interfere more or less with the proper performance of the respiratory function. As employed by Regnault and Reiset, it is adapted only to experiments on animals of small size. These give but an approximate idea, however, of the processes as they take place in the human subject. Pettenkofer constructed a chamber large enough to admit a man and allow perfect freedom of motion, eating, sleeping etc., into which air could be constantly introduced in definite quantity, and from which the products of respiration were constantly removed and estimated. This method had been adapted to the human subject on a small scale in 1843, by Scharling, but there was no arrangement for estimating the quantity of oxygen consumed.

Estimates of the absolute quantities of oxygen consumed or of carbon dioxide exhaled, based on analyses of the inspired and expired air, calculations from the average quantity of air changed with each respiratory act, and the average number of respirations per minute, are by no means so reliable as analyses showing the actual changes in the air, like those of Regnault and Reiset, provided the physiological conditions be fulfilled, Where there is so much multiplication and calculation, a very slight inaccuracy in the estimates of the quantities consumed or produced in a single respiration will make a large error in the estimate for a day or even for an hour. Bearing in mind all these sources of error, from the experiments of Valentin and Brunner, Dumas, Regnault and Reiset and others, a sufficiently accurate approximate estimate of the proportion of oxygen consumed by the human subject may be made. The air, which contains, when inspired, 20·81 parts of oxygen per 100, is found on expiration to contain but about 16 parts per 100. In other words, the volume of oxygen absorbed in the lungs is five per cent. or $\frac{1}{20}$ of the volume of air inspired. It is useful to extend this estimate as far as possible to the quantity of oxygen absorbed in a definite time; for the regulation of the supply of oxygen where many persons are assembled, as in public buildings, hospitals etc., is a question of great practical importance. Assuming that the average respirations per minute are eighteen, and that with each act, twenty cubic inches (327·7 c. c.) of air are changed, fifteen cubic feet (424·8 litres) of oxygen are consumed in the twenty-four hours, which represent three hundred cubic feet (8·5 cubic metres) of pure air. This is the minimum quantity of air which is actually used, making no allowance for any increase in the activity of the respiratory processes, which is liable to occur from various causes. To meet all the respiratory exigencies of the system, in hospitals, prisons etc., it has been found necessary to allow at least eight hundred cubic feet (22·65 cubic metres) of air for each person, unless the conditions be such that the air is changed with unusual frequency; for in addition to the actual loss of oxygen in the respired air, emanations from both the pulmonary and cutaneous surfaces are constantly taking place, which should be removed. In some institutions as much as twenty-five hundred cubic feet (70·79 cubic metres) of air are allowed for each person.

The quantity of oxygen consumed is subject to great variations, depending upon temperature, the condition of the digestive system, muscular activity etc. The following conclusions, the results of the observations of Lavoisier and Séguin, give at a glance the variations from the above-mentioned causes:

"1. A man, in repose and fasting, with an external temperature of about 90° Fahr. (32·5° C.), consumes 1,465 cubic inches (24 litres) of oxygen per hour.

"2. The same man, in repose and fasting, with an external temperature of 59° Fahr. (15° C.), consumes 1,627 cubic inches (26·66 litres) of oxygen per hour.

"3. The same man, during digestion, consumes 2,300 cubic inches (37·69 litres) of oxygen per hour.

"4. The same man, fasting, accomplishing the labor necessary to raise, in fifteen minutes, a weight of about 16 lb. 3 oz. (7·343 kilos.) to the height of 656 feet (200 metres) consumes 3,874 cubic inches (63·48 litres) of oxygen per hour.

"5. The same man, during digestion, accomplishing the labor necessary to raise, in fifteen minutes, a weight of about 16 lb. 3 oz. (7·343 kilos.) to the height of 692 feet (211·146 metres), consumes 5,568 cubic inches (91·24 litres) of oxygen per hour."

All who have experimented on the influence of temperature upon the consumption of oxygen, in the warm-blooded animals and in the human subject, have noted a marked increase at low temperatures. Immediately after birth the consumption of oxygen in the warm-blooded animals is relatively very slight. Buffon and Legallois have shown that just after birth, dogs and other animals will live for half an hour or longer under water; and cases are on record in which life has been restored in newborn children after seven, and it has been stated, after twenty-three hours of asphyxia (Milne-Edwards). During the first periods of existence the condition of the newly born is nearly that of a cold-blooded animal. The lungs are relatively very small, and it is some time before they fully assume their office. The muscular movements are hardly more than are necessary to take the small quantity of nourishment consumed at that period, and nearly all of the time is passed in sleep. There is also very little power of resistance to a low temperature. Although accurate researches regarding the comparative quantities of oxygen in the venous and arterial blood of the fœtus are wanting, it has been frequently observed that the difference in color is not so marked as it is after pulmonary respiration has become established. The direct researches of W. F. Edwards have shown that the absolute consumption of oxygen by very young animals is quite small; and the observations of Legallois, on rabbits, made every five days during the first month of life, show a rapidly increasing demand for oxygen.

The consumption of oxygen is greater in lean than in very fat animals, provided they be in perfect health. The consumption is greater, also, in carnivorous than in herbivorous animals; and in animals of different sizes, it is relatively much greater in those which are very small. In small birds, such as the sparrow, the relative quantity of oxygen absorbed was ten times greater than in the fowl (Regnault and Reiset).

During sleep the quantity of oxygen consumed is considerably diminished; and in hibernation it is so small, that Spallanzani could not detect any difference in the composition of the air in which a marmot, in a state of torpor, had remained for three hours. In experiments on a marmot in hibernation, Regnault and Reiset observed a reduction in the oxygen consumed to about $\frac{1}{30}$ of the ordinary quantity.

It has been shown by experiments, that the consumption of oxygen bears a nearly constant ratio to the production of carbon dioxide; and as the observations upon the influence of sex, the number of respiratory acts etc., on the activity of the respiratory processes have been made chiefly with reference to the carbon dioxide exhaled, these influences will be considered in connection with the products of respiration.

Experiments on the effect of increasing the proportion of oxygen in the air have led to varied results in the hands of different observers. Regnault and Reiset, whose observations on this point are generally accepted, did not discover any increase in the consumption of oxygen when this gas was largely in excess in the atmosphere.

The results of confining an animal in an atmosphere composed of twenty-one parts of oxygen and seventy-nine parts of hydrogen are very remarkable. When hydrogen is thus substituted for the nitrogen of the air, the consumption of oxygen is largely increased. Regnault and Reiset attributed this to the superior refrigerating power of the hydrogen; but a more rational explanation would seem to be in its greater diffusibility. Hydrogen is the most diffusible of all gases; and when introduced into the lungs in place of the nitrogen of the air, the vitiated air, charged with carbon dioxide, is undoubtedly more readily removed from the deep portions of the lungs, giving place to the mixture of hydrogen and oxygen. It is probably for this reason that the quantity of oxygen consumed is increased. It is probable that the nitrogen of the air plays an important part in the phenomena of respiration, by virtue of its degree of diffusibility.

In view of the great variations in the consumption of oxygen, dependent on different physiological conditions, such as digestion, exercise, temperature etc., it is impossible to fix upon any number which will represent, even approximately, the average quantity consumed per hour. The estimate arrived at by Longet, from a comparison of the results obtained by different reliable observers, is perhaps as near the truth as possible. This estimate puts the hourly consumption at 1,220 to 1,525 cubic inches (20 to 25 litres), "in an adult male, during repose and in normal conditions of health and temperature."

In passing through the lungs, the air, in addition to losing a certain proportion of its oxygen, undergoes the following changes:

1. Elevation in temperature.
2. Gain of carbon dioxide.
3. Gain of watery vapor.
4. Gain of ammonia.
5. Gain of a small quantity of organic matter.
6. Gain, and occasionally loss, of nitrogen.

The elevation in temperature of the air which has passed through the lungs has been studied by Gréhant. He found that with an external temperature of 72° Fahr. (22·22° C.), respiring seventeen times per minute, the air taken in by the nares, and expired by the mouth through an apparatus containing a thermometer carefully protected from external influences, marked a temperature of 95·4° Fahr. (35·22° C.). Taking in the air by the mouth, the temperature of the expired air was 93° Fahr. (33·89° C.). At the beginning of the expiration, Gréhant noted a temperature of 94° Fahr. (34·44° C.). After a prolonged expiration, the temperature was 96° Fahr. (35·55° C.). In these observations the temperature taken beneath the tongue was 98° Fahr. (36·67° C.)

*Exhalation of Carbon Dioxide.*—On account of the variations in the quantities of carbon dioxide exhaled at different times of the day, and particularly the great influence of the rapidity of the respiratory movements, it is difficult to fix upon any number that will represent the average proportion of this gas contained in the expired air. The same influences were found affecting the consumption of oxygen, and the same difficulties were experienced in forming an estimate of the proportion of this gas consumed. As it was assumed, after a comparison of the results obtained by different observers, that the volume of oxygen consumed is about five per cent. of the entire volume of air, it may be stated, as an approximation, that in the intervals of digestion, in repose and under normal conditions as regards the frequency of the pulse and respiration, the volume of carbon dioxide exhaled is about four per cent. of the volume of the expired air. As the volume of oxygen which enters into the composition of a definite quantity of carbon dioxide is equal to the volume of the carbon dioxide, it is seen that a certain quantity of oxygen disappears in respiration and is not represented in the carbon dioxide exhaled.

There are great differences in the proportion of carbon dioxide in the expired air, depending upon the time during which the air has remained in the lungs. This point was studied by Vierordt, in a series of ninety-four experiments made upon his own person, with the following results:

"When the respirations are frequent, the quantity of carbon dioxide expelled at each expiration is much less than in a slow expiration; but the quantity of carbon dioxide produced during a given time by frequent respirations is greater than that which is thrown off by slow expirations."

The air which escapes during the first part of an expiration is less rich in carbon dioxide than that which is last expelled and comes directly from the deeper portions of the lungs. Dividing, as nearly as possible, the expiration into two equal parts, Vierordt found, as the mean of twenty-one experiments, a percentage of 3·72 in the first part of the expiration and 5·44 in the second part.

Temporary arrest of the respiratory movements has a marked influence in increasing the proportion of carbon dioxide in the expired air, although the absolute quantity exhaled in a given time is diminished. In a number of experiments on his own person, Vierordt ascertained that the percentage of carbon dioxide becomes uniform in all parts of the respiratory organs, after holding the breath for forty seconds. Holding the breath after an ordinary inspiration, for twenty seconds, the percentage of carbon dioxide in the expired air was increased 1·73 above the normal standard; but the absolute quantity exhaled was diminished by 2·642 cubic inches (43·3 c. c.) After taking the deepest possible inspiration and holding the breath for one hundred seconds, the percentage was increased 3·08 above the normal standard; but the absolute quantity was diminished more than fourteen cubic inches (229·4 c. c.). Allen and Pepys noted that air which had passed nine or ten times through the lungs contained 9·5 per cent. of carbon dioxide.

Vierordt has given the following formula as representing the influence of the frequency of the respirations on the production of carbon dioxide: Taking 2·5 parts per hundred as representing the constant value of the gas exhaled by the blood, the increase over this proportion in the expired air is in exact ratio to the duration of the contact of the air and blood.

The absolute quantity of carbon dioxide exhaled in a given time is a more important subject of inquiry than the proportion contained in the expired air; for the latter varies with every modification in the number and extent of the respiratory acts, and the volume of breathing air is subject to great fluctuations and is very difficult of determination.

Among the most reliable observations on the quantity of carbon dioxide exhaled by the human subject in a definite time and the variations to which it is subject, are those of Andral and Gavarret and of Edward Smith. The observations of Lavoisier and Séguin, Prout, Davy, Dumas, Allen and Pepys, Scharling and others, do not seem to have fulfilled the necessary experimental conditions so completely. The observations of Andral and Gavarret were made on sixty-two persons of both sexes and different ages, and under identical conditions as regards digestion, time of the day, barometric pressure and temperature; and the observations on males between the ages of sixteen and thirty, between 1 and 2 P. M., under identical conditions of the digestive and muscular systems, each experiment lasting eight to thirteen minutes, showed an exhalation of about 1,220 cubic inches (20 litres) of carbon dioxide per hour.

Edward Smith employed the following method for the estimation of the carbon dioxide exhaled: He used a mask, fitting closely to the face, which covered only the air-passages. The air was admitted after having been measured by an ordinary, dry gas-meter. The expired air was passed through a drying apparatus, and the carbon dioxide was absorbed by a solution of potassium hydrate, arranged in a number of layers so as to present a surface of about seven hundred square inches (45 square decimetres), and was carefully weighed. This apparatus was capable of collecting all the carbon dioxide exhaled in an hour. The estimates were made for eighteen waking hours and six hours of sleep. The observations occupied ten minutes each and were made every hour and half-hour for eighteen hours. The average for the eighteen hours gave 20,082 cubic inches (329 litres) of carbon dioxide for the whole period. Observations during the six hours of sleep showed a total exhalation of 4,126 cubic inches (7·145 litres). This, added to the quantity exhaled during the day, gives as the total exhalation in the twenty-four hours, during complete repose, 24,208 cubic inches (about 14·24 cubic feet, or 336·145 litres), containing 7·144 oz. (202·47 grammes) of carbon. In view of the great variations in the exhalation of carbon dioxide, this estimate can be nothing more than an approximation.

One of the important modifying influences is muscular exertion, by which the production of carbon dioxide is largely increased. This would indicate a larger quantity during ordinary conditions of exercise, and a much larger quantity in the laboring classes. Dr. Smith has given the following approximate estimates of these differences:

| | | | |
|---|---|---|---|
| In quietude | 7·144 oz. | (202·47 grammes) | of carbon. |
| Non-laborious class | 8·68 " | (246·04 grammes) | " |
| Laborious class | 11·7 " | (331·61 grammes) | " |

In studying the variations in the exhalation of carbon dioxide, important imformation has been derived from experiments by many observers on the inferior animals, as well as from the observations of Dumas, Prout, Scharling, Pettenkofer and others, on the human subject. The principal conditions which influence the exhalation of this principle are the following: Age and sex; activity or repose of the digestive system; kind of diet; sleep; muscular activity; fatigue; moisture and surrounding temperature; season of the year.

*Influence of Age.*—In treating of the consumption of oxygen, it was stated that during the first few days of extraüterine existence, the demand for oxygen on the part of the system is very small. At this period there is a correspondingly feeble exhalation of carbon dioxide. It is well known that during the first hours and days after birth, the new being has little power of generating heat, needs constant protection from changes in temperature, and the voluntary movements are very imperfect. During the first few days, indeed, the infant does little more than sleep and take the small quantity of colostrum which is furnished by the mammary glands of the mother. While the animal functions are so imperfectly developed and until the alimentation becomes more abundant and the child begins to increase rapidly in weight, the quantity of carbon dioxide exhaled is very small.

After the respiratory function has become fully established, it is probable, from the greater number of respiratory movements in early life, that the production of carbon dioxide, in proportion to the weight of the body, is greater in infancy than in adult life. Direct observations, however, are wanting on this point.

The observations of Andral and Gavarret show the comparative exhalation of carbon dioxide in the male, between the ages of twelve and eighty-two, and give the results of a single observation at the age of one hundred and two years. They show an increase in the absolute quantity exhaled, from the age of twelve to thirty-two; a slight diminution, from thirty-two to sixty; and a considerable diminution, from sixty to eighty-two. Taking into consideration the increase in the weight of the body with age, it is evident that the respiratory activity is much greater in youth than in adult life, and there can be no doubt that there is a rapid diminution in the relative quantity of carbon dioxide produced in old age. Scharling, in a series of observations on a boy nine years of age, an adult of twenty-eight, and one of thirty-five years, showed that the respiratory activity in the child was nearly twice as great, in proportion to his weight, as the average in the adults.

*Influence of Sex.*—All observers have found a marked difference between the sexes, in favor of the male, in the proportion of carbon dioxide exhaled. Andral and Gavarret noted an absolute difference of about forty-five cubic inches (737·4 c. c.) per hour, but did not take into consideration the differences in the weight of the body. Scharling, taking the proportion exhaled to the weight of the body, noted a marked difference in favor of the male. The difference in muscular activity in the sexes is sufficient to account for the greater elimination of carbon dioxide in the male, for this substance is exhaled in proportion to the muscular development of the individual; but there is an important difference connected with the variations with age, which depends upon the condition of the generative system of the female. The absolute increase in the exhalation of carbon dioxide with age, in the female, is arrested at the time of puberty and remains stationary until the cessation of the menses, provided the menstrual flow occur with regularity (Andral and Gavarret). During this time the average exhalation per hour is 714 cubic inches (11·69 litres). After the cessation of the menses the quantity gradually increases, until, at the age of sixty, it amounts to 915 cubic inches (15 litres) per hour. From the age of sixty to eighty-two the quantity diminishes to 793 (13 litres), and finally to 670 cubic inches (about 11 litres). When the menses are suppressed, there is an increase in the exhalation of carbon dioxide, which continues until the flow becomes reëstablished. In a case of pregnancy observed by Scharling the exhalation was increased to about 885 cubic inches (14·5 litres).

*Influence of Digestion.*—Almost all observers agree that the exhalation of carbon dioxide is largely increased during digestion. Lavoisier and Séguin found that in repose and fasting, the quantity exhaled per hour was 1,210 cubic inches (19·82 litres), which was raised to 1,800 and 1,900 (29·5 and 31·14 litres) during digestion. A series of observations on this point was made by Vierordt upon his own person. Taking his dinner between 12·30 and 1 P. M., having noted the frequency of the pulse and respirations and the exhalation of carbon dioxide at 12 M., he found at 2 P. M., the pulse and respirations increased in frequency, the volume of expired air augmented, and the carbon dioxide exhaled increased from 15·77 to 18·22 cubic inches (258·43 to 298·6 c. c.) per minute. In order to ascertain that this variation did not depend upon the time of day, independently of the digestive process, he made a comparison at 12 M., at 1 and at 2 P. M. without taking food, which showed no notable variation, either in the pulse, number of respirations, volume of expired air or quantity of carbon dioxide exhaled.

The effect of inanition is to gradually diminish the exhalation of carbon dioxide. Bidder and Schmidt noted the daily production in a cat which was subjected to eighteen days of inanition, at the end of which time it died. The quantity diminished gradually from day to day, until just before death it was reduced a little more than one-half. Edward Smith noted in his own person the influence of a fast of twenty-seven hours. There was a marked dimunition in the quantity of air respired, in the quantity of vapor exhaled, in the number of respirations and in the rapidity of the pulse. The exhalation of carbon dioxide was diminished one-fourth. An important point in this observation was that the quantity was as small four and a half hours after eating as at the end of the twenty-seven hours.

*Influence of Diet.*—The most extended series of investigations on the influence of diet upon the absolute quantity of carbon dioxide exhaled are those of Edward Smith. This observer made a large number of experiments on the influence of various kinds of food, and extended his inquiries into the influence of certain beverages, such as tea, coffee, cocoa, malt liquors and fermented liquors. He divided food into two classes: one which increases the exhalation of carbon dioxide, which he called respiratory excitants, and the other, which diminishes the exhalation, he called non-exciters. The following are the results of a large number of observations upon four persons:

"The excito-respiratory are nitrogeneous food, milk and its components, sugars, rum, beer, stout, the cereals, and potato.

"The non-exciters are starch, fat, certain alcoholic compounds, the volatile elements of wines and spirits, and coffee-leaves.

"Respiratory excitants have a temporary action; but the action of most of them commences very quickly, and attains its maximum within one hour.

"The most powerful respiratory excitants are tea and sugar; then coffee, rum, milk, cocoa, ales, and chiccory; then casein and gluten, and lastly, gelatin and albumen. The amount of action was not in uniform proportion to their quantity. Compound aliments, as the cereals, containing several of these substances, have an action greater than that of any of their elements.

"Most respiratory excitants, as tea, coffee, gluten, and casein, cause an increase in the evolution of carbon greater than the quantity which they supply, while others, as sugar, supply more than they evolve in this excess, that is, above the basis. No substance containing a large amount of carbon evolves more than a small portion of that carbon in the temporary action occurring above the basis-line, and hence a large portion remains unaccounted for by these experiments."

The comparative observations upon the four persons who were the subjects of experiment demonstrated one very important fact; namely, that the action of different kinds of food upon respiration is modified by idiosyncrasies and the tastes of different individuals.

The following are the results of observations upon the effects of different alcoholic beverages taken during the intervals of digestion:

"Brandy, whiskey, and gin, and particularly the latter, almost always lessened the respiratory changes recorded, while rum as commonly increased them. Rum-and-milk had a very pronounced and persistent action, and there was no effect on the sensorium. Ale and porter always increased them, while sherry wine lessened the quantity of air inspired, but slightly increased the carbonic acid evolved.

"The volatile elements of alcohol, gin, rum, sherry, and port-wine, when inhaled, lessened the quantity of carbonic acid exhaled, and usually lessened the quantity of air inhaled. The effect of fine old port-wine was very decided and uniform; and it is known that wines and spirits improve in aroma and become weaker in alcohol by age. The excito-respiratory action of rum is probably not due to its volatile elements."

From these facts it would seem that the most constant effect of alcohol and of alcoholic liquors, such as wines and spirits, is to diminish the exhalation of carbon dioxide. This effect is almost instantaneous, when the articles are taken into the stomach fasting; and when taken with the meals, the increase in carbon dioxide, which habitually accompanies the process of digestion, is materially lessened. Rum, which was found to be a respiratory excitant, is an exception to this rule. Malt liquors seem to increase the exhalation of carbon dioxide. "The action of pure alcohol was much more to increase than to lessen the respiratory changes, and sometimes the former effect was well pronounced."

*Influence of Sleep.*—All who have directed attention to the influence of sleep upon the respiratory products have noted a marked diminution in the exhalation of carbon dioxide. According to Edward Smith, the quantity during the night is to the quantity during the day, in complete repose, as ten to eighteen.

It has already been stated that there is great diminution in the quantity of oxygen consumed in hibernating animals while in a torpid condition. Regnault and Reiset found that a marmot in hibernation consumed only $\frac{1}{30}$ of the oxygen ordinarily appropriated in the active condition. In the same animal they noted an exhalation of carbon dioxide equal to but little more than half the weight of oxygen absorbed.

*Influence of Muscular Activity.*—Vierordt, in a number of observations on the human subject, ascertained that moderate exercise increased the average quantity of air respired per minute by nearly nineteen cubic inches (311·4 c. c.), and that there was an increase of 1·197 cubic inch (19·63 c. c.) per minute in the absolute quantity of carbon dioxide exhaled.

The results of the experiments of Dr. Edward Smith on the influence of exercise are as follows:

In walking at the rate of two miles (3·22 kilometres) per hour, the exhalation of carbon dioxide during one hour was equal to the quantity produced during 1$\frac{4}{5}$ hour of repose with food or 2$\frac{1}{2}$ hours of repose without food.

Walking at the rate of three miles (4·828 kilometres) per hour, one hour was equal to 2$\frac{3}{4}$ hours with food or 3$\frac{1}{2}$ hours without food.

One hour's labor at the tread-wheel, while actually working the wheel, was equal to 4$\frac{1}{2}$ hours of rest with food or 6 hours without food.

It has been observed, however, that when muscular exertion is carried so far as to produce great fatigue and exhaustion, the exhalation of carbon dioxide is notably diminished.

*Influence of Moisture and Temperature.*—It has been shown that the exhalation of carbon dioxide is greater in a moist than in a dry atmosphere (Lehmann). It has also been ascertained that the exhalation is much greater at low than at high temperatures, within the limits of heat and cold that are easily endured, amounting, according to the experiments of Vierordt on the human subject, to an increase of about one-sixth, under the influence of a moderate diminution in temperature. It was found, also, that the quantity of air taken into the lungs was slightly increased at low temperatures.

*Influence of the Season of the Year, etc.*—It has been shown by the researches of Edward Smith, that spring is the season of the greatest, and fall the season of the least activity of the respiratory function.

The months of maximum are January, February, March and April.

The months of minimum are July, August and a part of September.

The months of decrease are June and July.

The months of increase are October, November and December.

Observations on the influence of barometric pressure have not been sufficiently definite in their results to warrant any exact conclusions.

Some physiologists have attempted to fix certain hours of the day when the exhalation of carbon dioxide is at its maximum and at its minimum; but the respiratory activity is influenced by such a variety of conditions that it is impossible to do this with any degree of accuracy.

### Relations between the Quantity of Oxygen consumed and the Quantity of Carbon Dioxide exhaled.

Oxygen unites with carbon in a certain proportion to form carbon dioxide, the volume of which is equal to the volume of the oxygen which enters into its composition. It is possible, therefore, to study the relations of the volumes of these gases in respiration, by simply comparing the volumes of the inspired and expired air. It is now generally recognized that the volume of air expired is less, at an equal temperature, than the volume of air inspired. Assuming, then, that the changes in the expired air, as regards nitrogen and all gases except oxygen and carbon dioxide, are insignificant, it must be admitted that a certain quantity of the oxygen consumed by the economy is unaccounted for by the oxygen which enters into the composition of the carbon dioxide exhaled. It has already been stated that $\frac{1}{70}$ to $\frac{1}{50}$ (1·4 to 2 per cent.) of the inspired air is lost in the lungs; or it may be said in general terms, that the oxygen absorbed is equal to about five per cent. of the volume of air inspired, and the carbon dioxide exhaled, only about four per cent. A part of the deficiency in volume of the expired air is to be accounted for, then, by a deficiency in the exhalation of carbon dioxide.

The experiments of Regnault and Reiset have an important bearing on the question under consideration. As these observers were able to accurately measure the entire quantities of oxygen consumed and carbon dioxide produced in a given time, the relation between the two gases was kept constantly in view. They found great variations in this relation, mainly dependent upon the regimen of the animal. The total loss of oxygen was found to be much greater in carnivorous than in herbivorous animals; and in animals that could be subjected to a mixed diet, by regulating the food this was made to vary between the two extremes. The mean of seven experiments on dogs showed that for every 1,000 parts of oxygen consumed, 745 parts were exhaled in the form of carbon dioxide. In six experiments on rabbits, the mean was 919 for every 1,000 parts of oxygen.

In animals fed on grains, the proportion of carbon dioxide exhaled was greatest, sometimes passing a little beyond the volume of oxygen consumed.

"The relation is nearly constant for animals of the same species which are subjected to a perfectly uniform alimentation, as is easy to realize as regards dogs; but it varies notably in animals of the same species, and in the same animal, submitted to the same regimen, but in which we can not regulate the alimentation, as in fowls."

When herbivorous animals were entirely deprived of food, the relation between the gases was the same as in carnivorous animals.

The final result of the experiments of Regnault and Reiset was that the "relation between the oxygen contained in the carbon dioxide and the total oxygen consumed, varies, in the same animal, between 0·62 and 1·04, according to the regimen to which it is subjected." These observations on animals have been confirmed in the human subject by Doyère, who found a great variation in the relations of the two gases in respiration; the volume of carbon dioxide exhaled varying between 0·862 and 1·087 for 1 part of oxygen consumed.

As regards the destination of the oxygen which is not represented in the carbon dioxide exhaled, it is certain that a part of it, at least, unites with hydrogen to form water, this contributing to the production of animal heat, a question that will be fully discussed in another connection.

The variations in the relative volumes of oxygen consumed and carbon dioxide produced in respiration are not favorable to the hypothesis that the carbon dioxide is always a result of the direct action of oxygen upon the carbohydrates and fats. Such a definite relation between these two gases can not be assumed to exist, in view of the fact that carbon dioxide may be given off by the tissues in the absence of oxygen.

Many of the points that have been considered with relation to the variations in the exhalation of carbon dioxide have been investigated in Pettenkofer's chamber, and the results very nearly correspond with the observations quoted from Scharling, Edward Smith and others.

*Sources of Carbon Dioxide in the Expired Air.*—All the carbon dioxide in the expired air comes from the venous blood, where it exists in two forms; in a free state in simple solution, or at least in a state of very feeble combination, and in union with bases, forming the carbonates and bicarbonates. The fact that carbon dioxide, as regards the quantity absorbed by the blood, does not obey, in all regards, the laws which regulate the absorption of gases by liquids under different conditions of pressure, has led some physiologists to regard all of this gas as existing in the blood in a condition of chemical combination; the greater part being very loosely united with certain other substances, and a small quantity of that which is thrown off in the expired air being in a condition of union much more stable. The greater part of the carbon dioxide exhaled comes from the plasma, where it is in feeble combination, if it be not simply in solution. Another and a smaller part is probably set free by the action of the oxyhæmaglobine, which is distinctly acid. It has been shown that more carbon dioxide can be extracted by means of a vacuum from the entire blood than from the serum; and this gas is more readily extracted from arterial than from venous blood. The mechanism by which the carbon dioxide is discharged from the venous blood is probably the following:

Carbon dioxide is carried from the tissues to the lungs, in the venous blood. Here it exists mainly in the plasma, a small quantity, only, existing in the corpuscles. As the venous blood passes through the lungs, the greater part of the carbon dioxide of the plasma either simply diffuses from the blood into the air-cells or passes out by a process known to chemists as dissociation (Deville). It is certain that the oxyhæmaglobine, which is constantly forming in the lungs, assists materially in this process.

There can be no doubt with regard to the existence of an acid of some kind in the lungs, which possibly decomposes a portion of the bicarbonates of the blood, in ordinary respiration. When sodium bicarbonate is injected into the jugular of a living animal, a rabbit, for example, it is decomposed as fast as it gets to the lungs, and carbon dioxide is evolved. This experiment produces no inconvenience to the animal when the bicarbonate is introduced slowly; but when it is injected in large quantity, the evolution of gas in the lungs is so great as to fill the pulmonary structure and even the heart and great vessels, and death is the result (Bernard).

*Exhalation of Watery Vapor.*—From a large number of observations on his own person and upon eight others, collecting the water by sulphuric acid, Valentin made the following estimates of the quantities of water exhaled from the lungs in twenty-four hours:

In his own person the exhalation in twenty-four hours was 5,934 grains (384·48 grammes).

In a young man of small size the quantity was 5,401 grains (350 grammes).

In a student rather above the ordinary height the quantity was 11,929 grains (773 grammes).

The mean of his observations gave a daily exhalation of 8,333 grains (540 grammes), or about a pound and a half.

The extent of respiratory surface has a marked influence on the quantity of watery vapor exhaled. This fact is very well shown by a comparison of the exhalation in the adult and in old age, as in advanced life the extent of respiratory surface is much diminished. Barral found the exhalation in an old man less than half that of the adult. It is evident that the absolute quantity of vapor exhaled is increased when respiration is accelerated. The quantity of water in the blood also exerts an important influence. Valentin found that the pulmonary transpiration was more than doubled in a man immediately after drinking a large quantity of water.

The vapor in the expired air is derived from the entire surface over which the air passes in respiration, and not exclusively from the air-cells. The air which passes into the lungs derives a certain quantity of moisture from the mouth, nares and trachea. The great vascularity of the mucous membranes in these situations, as well as of the air-cells, and the great number of mucous glands which they contain, serve to keep the respiratory surfaces constantly moist. This is important, for only moist membranes allow the free passage of gases, which is of course essential to the process of respiration.

*Exhalation of Ammonia, Organic Matter etc.*—A small quantity of ammonia is exhaled by the lungs in health, and this is increased in certain diseases, particularly in uræmia. Its characters in the expired air are frequently so marked, that patients who are entirely unacquainted with the pathology of uræmia sometimes recognize an ammoniacal odor in their own breath.

The pulmonary surface exhales a small quantity of organic matter. This has never been collected in sufficient quantity for analysis, but its presence may be demonstrated by the fact that a sponge completely saturated with the exhalations from the lungs, or the vapor from the lungs condensed in a glass vessel, will undergo putrefaction, which is a property distinctive of organic substances.

It is well known that certain substances which are but occasionally found in the blood may be eliminated by the lungs. Certain odorous matters in the breath are constant in those who take liquors habitually in considerable quantity. The odor of garlics, onions, turpentine and of many other articles taken into the stomach, may be recognized in the expired air.

The lungs eliminate certain gases which are poisonous in very small quantities when they are absorbed in the lungs and carried to the general system in the arterial blood. Hydrogen monosulphide, which produces death in a bird when it exists in the atmosphere in the proportion of one to eight hundred, may be taken in solution into the stomach with impunity and even be injected into the venous system; in both instances being eliminated by the lungs with great promptness and rapidity (Bernard). The lungs, while they present an immense and rapidly absorbing surface for volatile poisonous substances, are capable of relieving the system of some of these by exhalation when they find their way into the veins.

*Exhalation of Nitrogen.*—The most accurate direct experiments, particularly those of Regnault and Reiset, show that the exhalation of a small quantity of nitrogen is a nearly constant respiratory phenomenon. As the result of a large number of experiments, these observers came to the conclusion that when animals are subjected to their habitual regimen, they exhale a quantity of nitrogen equal in weight to $\frac{1}{100}$ or $\frac{1}{50}$ of the weight of oxygen consumed. In birds, during inanition, they sometimes observed an absorption of nitrogen, but this was rarely seen in mammals. Boussingault, estimating the nitrogen taken into the body and comparing it with the entire quantity discharged, arrived at the same results in experiments upon a cow. Barral, by the same method, confirmed these observations by experiments on the human subject. Notwithstanding the conflicting testimony of physiologists, there can be little doubt that under ordinary physiological conditions, there is an exhalation of a small quantity of nitrogen by the lungs.

## Changes of the Blood in Respiration (Hæmatosis).

It is to be expected that the blood, receiving, on the one hand, all the products of digestion, and on the other, the products of disassimilation, or wear of the tissues, connected with the lymphatic system, and exposed to the action of the air in the lungs, should present important differences in composition in different parts of the vascular system.

In the first place, there is a marked difference in color, composition and properties, between the blood in the arteries and in the veins; the change from venous to arterial blood being effected almost instantaneously in its passage through the lungs. The blood which goes to the lungs is collected from all parts of the body and presents great differences in its composition in different veins. In some veins it is almost black, and in some it is nearly as red as in the arteries. In the hepatic vein it contains sugar, and its nitrogenized constituents and the corpuscles are diminished; in the portal vein, during digestion, it contains matters absorbed from the alimentary canal; and finally, there is every reason to suppose that parts which require different substances for their nutrition and produce different excrementitious matters exert different influences on the constitution of the blood which passes through them. After this mixture of different kinds of blood has been collected in the right side of the heart and passed through the lungs, it is returned to the left side and sent to the system, thoroughly changed and renovated, and as arterial blood, it has a nearly uniform composition. The change, therefore, which the blood undergoes in its passage through the lungs, is the transformation of the mixture of venous blood from all parts of the organism into a fluid of uniform character which is capable of nourishing every tissue and organ of the body.

The capital phenomena of respiration, as regards the air in the lungs, are loss of oxygen and gain of carbon dioxide, the other phenomena being comparatively unimportant. As the blood is capable of absorbing gases, the essential changes which this fluid undergoes in respiration are to be looked for in connection with the proportions of oxygen and carbon dioxide before and after it has passed through the lungs.

The change of color in the blood from dark-blue to red, in its passage through the lungs, was recognized by Lower, Goodwyn and others, as due to the action of the air, long before the discovery of oxygen. Since the discovery of oxygen, it has been ascertained that this is the only constituent of the air which is capable of arterializing the blood. Priestley showed that venous blood is not changed in color by nitrogen, hydrogen or carbon dioxide; while all these gases, by displacing oxygen, will change the arterial blood from red to black. Carbon monoxide, although it is not a respirable gas and does not properly arterialize the blood, changes it from black to red.

The elements of the blood which absorb the greater part of the oxygen are the red corpuscles. While the plasma will absorb, perhaps, twice as much gas as pure water, it has been shown that the volume of oxygen fixed by the corpuscles is about twenty-five times that which is dissolved in the plasma (Fernet, Lothar Meyer).

*Comparison of the Gases in Venous and Arterial Blood.*—The demonstration of the fact that oxygen and carbon dioxide exist in the blood, with a knowledge of the relative proportion of these gases in the blood before and after its passage through the lungs, are points hardly second in importance to the relative composition of the air before and after respiration. The idea enunciated by Mayow, about two hundred years ago, that "there is something in the air, absolutely necessary to life, which is conveyed into the blood," except that the vivifying principle was not named or its other properties described, expresses what is now regarded as one of the great objects of respiration. This is even more strictly in accordance with facts than the idea of Lavoisier, who supposed that all the chemical processes of respiration took place in the lungs. Mayow also described the evolution of gas from blood placed in a vacuum. Many observers have since succeeded in extracting gases from the blood by various processes; but notwithstanding this, before the experiments of Magnus, in 1837, many denied the existence of free gases in the blood.

*Analysis of the Blood for Gases.*—There were certain grave sources of error in the method employed by Magnus, which render his observations of little value, except as demonstrating that oxygen, carbon dioxide and nitrogen may be extracted by the air-pump from both arterial and venous blood. The only source of error in the results which he fully recognized lay in the difficulty in extracting the entire quantity of gas; but a careful study of his essay shows another element of inaccuracy which is even more important. The relative quantities of oxygen and carbon dioxide in any single specimen of blood present great variations, dependent upon the length of time that the blood has been allowed to stand before the estimate of the gases is made. As it is difficult to make this estimate immediately after the blood is drawn, on account of the froth produced by agitation with a gas when the method by displacement is employed, and the bubbling of the gas when extracted by the air-pump, the objection is very serious. It is necessary to wait until the froth has subsided before attempting to make an accurate estimate of the volume of gas given off. This fact is illustrated by one of the published observations of Magnus upon three different specimens of human blood. In this observation the specimens of blood were thoroughly mixed with hydrogen. The excess of carbon dioxide found twenty-four hours after, over the quantity found six hours after, in two specimens, was a little more than fifty per cent., while in one specimen it is very nearly one hundred per cent. In these analyses the proportion of oxygen was not given. The question naturally arises as to the source of the carbon dioxide which was evolved during the last eighteen hours of the observation. The question is readily solved by certain experiments, which are by no means of recent date, although the results of these observations have been confirmed by modern investigations. A number of years ago, Spallanzani demonstrated that in common with other parts of the body, fresh blood has, of itself, the property of consuming oxygen; and W. F. Edwards has shown that the blood will exhale carbon dioxide. In 1856, Harley found that blood, kept in contact with air in a closed vessel for twenty-four hours, consumed oxygen and gave off carbon dioxide. More recently, Bernard has shown that for a certain time after the blood is drawn from the vessels, it will continue to consume oxygen and exhale carbon dioxide. If all the carbon dioxide be removed from a specimen of blood by treating it with hydrogen, and if it be allowed to stand for twenty-four hours, another portion of gas can be removed by again treating the blood with hydrogen, and still another quantity, by treating it with hydrogen a third time. From these facts it is clear that in the experiment of Magnus, the excess of carbon dioxide involved a post-mortem consumption of oxygen; and no analyses made in the ordinary way, by displacement with hydrogen or by the air-pump, in which the blood is allowed to remain in contact with oxygen for a number of hours, can be accurate. The only process which can give a rigorous estimate of the relative quantities of oxygen and carbon dioxide in the blood is one in which the gases can be estimated without allowing the blood to stand, or in which the formation of carbon dioxide, at the expense of the oxygen in the specimen, is prevented. All others will give a less quantity of oxygen and a greater quantity of carbon dioxide than exists in the blood circulating in the vessels or immediately after it is drawn from the body.

Carbon monoxide, one of the most active of the poisonous gases, has a remarkable affinity for the blood-corpuscles. When taken into the lungs, it is absorbed by and becomes fixed in the corpuscles, preventing the consumption of oxygen and the production of carbon dioxide, which normally take place in the capillary system and which are indispensable conditions of nutrition. The mechanism of poisoning by the inhalation of this gas is by its fixation in the blood-corpuscles, their consequent paralysis, and the arrest of their action as oxygen-carriers. As it is the continuance of this transformation of oxygen into carbon dioxide, after the blood is drawn from the vessels, which interferes with the ordinary analysis of the blood for gases, it would seem possible to extract all the oxygen by immediately saturating the blood with carbon monoxide. The experiments of Bernard on this point are conclusive. He ascertained that by mixing carbon monoxide in sufficient quantity with a specimen of fresh arterial blood, in about two hours, all the oxygen which it contained was displaced. Introducing a second quantity of carbon monoxide after two hours and leaving it in contact with the blood for an hour, a quantity of oxygen was removed so small that it might be disregarded. A third experiment on the same blood failed to disengage any oxygen or carbon dioxide.

The view entertained by Bernard of the action of carbon monoxide in displacing the oxygen of the blood is that the former gas has a remarkable affinity for the blood-corpuscles, in which nearly all the oxygen is contained, and when brought in contact with them unites with the hæmaglobine, setting free the oxygen, in the same way that an acid entering into the composition of a salt is set free by any other acid which has a stronger affinity for the base. There is every reason to suppose that this view is correct, as carbon monoxide is much less soluble than oxygen and as it has the property of disengaging this gas only from the blood, leaving the other gases still in solution. In drawing the blood for analysis, Bernard took the fluid directly from the vessels by a syringe and passed it under mercury into a tube, in such a way that it did not come in contact with the air. In this tube, which was graduated, the blood was brought in contact with carbon monoxide, which displaced the oxygen from the corpuscles and prevented the formation of carbon dioxide at the expense of a portion of the oxygen.

As carbon monoxide displaces the oxygen alone, it is necessary to resort to some other process to disengage the other gases contained in the blood. Modern experimenters, Ludwig, Lothar Meyer and others, have made use of the mercurial gas-pumps, either of Ludwig or of Pflüger, in which all the gases of the blood are disengaged by removing the atmospheric pressure. By means of a "froth-chamber," the gases can be collected and analyzed, with but little loss of time; but it is probable that there is always a slight error in estimates, made in this way, of the relative proportions of oxygen and carbon dioxide, the proportion of oxygen being too small, and of carbon dioxide, too large. Nevertheless, the results obtained by this method correspond pretty closely with what is known of the nature of the respiratory process; and analyses of the blood taken at different periods show variations in the quantities of oxygen in the arterial blood and of carbon dioxide in the venous blood, corresponding with some of the variations which have been noted in the loss of oxygen and gain of carbon dioxide in the air in respiration. Nearly all the gases contained in the blood may be disengaged by means of the gas-pump, but according to most observers, a small quantity of carbon dioxide remains in the blood in combination. This may be removed by the introduction into the apparatus of a small quantity of tartaric acid. It was justly remarked by Bert, that as the apparatus for the exhaustion of air has been made more and more nearly perfect, the quantity of carbon dioxide in combination has seemed less and less. By far the greatest quantity of the excrementitious carbon dioxide in the blood is extracted by the removal of atmospheric pressure in the most carefully perfected apparatus.

According to Bernard, arterial blood, while an animal is fasting, contains nine to eleven parts per hundred in volume of oxygen. In full digestion, the proportion is raised to seventeen, eighteen or even twenty parts per hundred. The proportion varies in different animals, being much greater, for example, in birds than in mammals. The quantity of carbon dioxide is even more variable than the quantity of oxygen. During digestion there are five to six parts per hundred of carbon dioxide in the arterial blood. During the intervals of digestion this quantity is reduced to almost nothing; and after fasting for twenty-four hours, frequently not a trace is to be discovered.

The quantity of carbon dioxide varies considerably in different parts of the venous system. It is well known that the venous blood coming from some glands is dark, during the intervals of secretion, and nearly as red as arterial blood, during secretion. In the venous blood from the submaxillary gland of a dog, Bernard found 18·07 per cent. of carbon dioxide during repose and 10·14 per cent. during secretion. The blood coming from the muscles is the darkest in the body and contains the greatest quantity of carbon dioxide. The quantity of carbon dioxide is increased in the venous blood during digestion; and it is owing to this that the gas then exists in quantity in the arterial blood. Bearing in mind the fact that the proportion of gases in the arterial and venous blood varies considerably under different conditions of the system and that it is variable in the blood of different veins, the following general statement, taken from Bert (1870), may be accepted as representing the average results obtained up to that time. The most recent results, particularly those obtained by German observers, present no important variations from this average:

| | Oxygen. | Carbon dioxide disengaged by a vacuum. | Carbon dioxide in combination. | Carbon dioxide, total. | Nitrogen. | Total gas in volume per 100. |
|---|---|---|---|---|---|---|
| "Arterial blood. | 15·03 | 27·99 | 1·15 | 29·14 | 1·60 | 45·77 |
| Venous blood. | 8·17 | 31·27 | 2·38 | 33·65 | 1·37 | 43·19 |

"If the blood coming from different parts of the body be now examined, it is found that the blood of the hepatic veins is poorer in oxygen and richer in carbon dioxide than the general venous blood; that the blood of the portal vein presents the same characters to a higher degree; that the blood of the muscles in contraction presents the same relations as compared with the blood of muscles in repose or paralyzed; that, on the other hand, the blood of the glands has more oxygen during their activity than during their repose.

"In comparing the venous blood of the right side of the heart with the arterial blood of the left side, it is found that the latter is richer in oxygen and poorer in carbon dioxide. In examining this more closely, it is seen that the difference in the oxygen is greater than in the carbon dioxide; this being in accordance with the well known fact that animals absorb more oxygen than is equivalent to the carbon dioxide exhaled."

These facts coincide with the views which are now held regarding the essential processes of respiration. The blood going to the lungs contains carbon dioxide and but a small proportion of oxygen. In the lungs carbon dioxide is given off, appearing in the expired air, and the oxygen which disappears from the air is carried away by the arterial blood.

*Nitrogen of the Blood.*—As far as is known, nitrogen has no important office connected with respiration. There is sometimes a slight exhalation of this gas by the lungs, and analyses have demonstrated its existence in solution in the blood. Magnus found generally a larger proportion in the arterial than in venous blood, although in one instance there was a large proportion in the venous blood. It is not absolutely certain whether the nitrogen which exists in the blood be derived from the air or from the tissues. Its almost constant exhalation in the expired air would lead to the supposition that it is produced in small quantity in the system or is supplied by the food. There is no evidence that nitrogen enters into combination with the blood-corpuscles. It exists simply in solution in the blood, which is capable of absorbing about ten times as much as can be absorbed by pure water. Nothing is known with regard to the relations of the free nitrogen of the blood to the processes of nutrition.

*Condition of the Gases in the Blood.*—It is now generally admitted that the oxygen of the blood exists, not in simple solution, but in a condition of combination with the hæmaglobine of the blood-corpuscles. In studying the composition of the corpuscles, it has been seen that when air is admitted to venous blood, oxygen unites with the hæmaglobine, forming oxyhæmaglobine. Carbon monoxide, which has a great affinity for the corpuscles, displaces almost immediately all the oxygen which the blood contains. When the corpuscles are destroyed, as they may be readily by receiving fresh blood into a quantity of pure water, the red color is instantly changed to black.

The condition under which carbon dioxide exists in the blood has already been considered in connection with the mechanism of its passage from the venous blood into the air-cells. This gas is contained chiefly in the plasma; a small quantity, however, probably exists in the red blood-corpuscles. The greatest part of the carbon dioxide of the plasma is either in simple solution or in a condition of very feeble combination, the exact nature of which is not understood. It has been ascertained that the blood-serum will absorb much more carbon dioxide than is absorbed under similar conditions by pure water. It has been shown, also, that neutral sodium phosphate increases to a remarkable degree the quantity of carbon dioxide that can be absorbed by any liquid. It is probable that a small part of the carbon dioxide of the plasma, which passes into the expired air, is in combination with sodium in the form of sodium bicarbonate.

*General Differences in the Composition of Arterial and Venous Blood.*—All observers agree that there are certain marked differences in the composition of arterial and venous blood, aside from the proportion of gases. The arterial blood contains less water and is richer in organic and in most inorganic constituents than the venous blood. It also contains a larger proportion of corpuscles. It is more coagulable and offers a larger and firmer clot than the clot of venous blood. The only constituents which are constantly more abundant in venous blood are water and the alkaline carbonates. According to Longet, 10,000 parts of venous blood contained 12·3 parts of carbon dioxide combined, and the same quantity of arterial blood contained but 8·3 parts. The deficiency of water in the blood which comes from the lungs is readily explained by the escape of watery vapor in the expired air.

An important distinction between arterial and venous blood is that the former has a uniform composition in all parts of the arterial system, while the composition of the latter varies very much in the blood coming from different organs. Arterial blood is capable of carrying on the processes of nutrition, while venous blood is not, and it can not even circulate freely in the systemic capillaries.

*Relations of Respiration to Nutrition, etc.*—It has been demonstrated that all tissues, so long as they retain their absolute integrity of composition, have the property of appropriating oxygen and exhaling carbon dioxide, independently of the presence of blood; and that the arterial blood carries oxygen from the lungs to the tissues, there gives it up, and receives carbon dioxide, which is carried by the venous blood to the lungs, to be exhaled. This fact alone shows that respiration is inseparably connected with the general act of nutrition. Its processes must be studied, therefore, as they take place in the tissues and organs of the body.

Oxygen taken from the air is immediately absorbed by the blood and enters into the composition of the red corpuscles. Part of the oxygen disappears in the red corpuscles themselves, and carbon dioxide is given off. To how great an extent this takes place, it is impossible to say; but it is evident, even from a study of the methods of analysis of the blood for gases, that the property of absorbing oxygen and giving off carbon dioxide, which belongs to the tissues, is possessed as well by the red corpuscles. During life it is not possible to determine how far this takes place in the blood and how far it occurs in the tissues. The theory has been proposed that the respiratory change takes place in the blood as it circulates; but the avidity of the tissues for oxygen and the readiness with which they exhale carbon dioxide leave no room for doubt that much of this change is effected in their substance.

Oxygen, carried by the blood to the tissues, is appropriated and consumed in their substance, together with the nutritive materials contained in the circulating fluid. Physiologists are acquainted with some of the laws which regulate its consumption, but have not been able to ascertain the exact nature of the changes which take place. All that can be said definitely on this point is that oxygen unites with the organic constituents of the body, satisfying the "respiratory sense" and supplying an imperative want which is felt by all animals and which extends to all parts of the organism. After its absorption, oxygen is lost in the processes of nutrition. There is no evidence in favor of the view that oxygen unites directly with carbonaceous matters in the blood which it meets in the lungs, and by direct union with carbon, forms carbon dioxide.

That carbon dioxide makes its appearance in the blood itself, produced in the red corpuscles, has been abundantly proved by observations already cited, although it is impossible to determine to what extent this takes place during life. It is likewise a product of the physiological wear of the tissues, is absorbed by the blood circulating in the capillaries and is conveyed by the veins to the right side of the heart. It has been shown that its production is not immediately dependent upon the absorption of oxygen, for its formation continues in an atmosphere of hydrogen or of nitrogen. It is most reasonable to consider the carbon dioxide thus formed as a product of excretion. The fact that it may easily be produced artificially, out of the body, does not demonstrate that its formation in the body is as simple as when it is formed by the process of combustion. It may be possible at some future time to produce artificially all the excremetitious principles, as has already been done in the case of urea; but it can not be assumed that the mode of formation of carbon dioxide, as one of the phenomena of nutrition, is precisely the same as when it is made by chemical manipulations.

## The Respiratory Sense.

It is generally admitted that there exists in the system what may be regarded as a respiratory sense, which operates upon the respiratory nerve-centre and gives rise to the involuntary movements of respiration; and that this sense is exaggerated by anything which interferes with respiration, and is then conveyed to the brain, where it is appreciated as dyspnœa and finally as the sense of suffocation. An exaggeration of the respiratory sense constitutes a sense of oppression, which is referred to the lungs; but it can not be assumed, from sensations only, that the sense of want of air is really situated in the lungs.

At the present day it is hardly necessary to discuss the views of those who attributed the sense of want of air, at least in its exaggerated form, to an accumulation of carbon dioxide in the lungs (Marshall Hall), distention of the right cavities of the heart (Bérard), or to impressions conveyed to the medulla oblongata, exclusively by the pneumogastric nerves. These theories have long since been disproved and are now merely of historical interest. Volkmann, in 1841, advanced the view that this sense is dependent upon a deficiency of oxygen in the tissues, producing an impression which is conveyed to the medulla oblongata by the nerves of general sensibility. By a series of experiments, this observer disproved the view that the respiratory sense always originates in the lungs and is transmitted by the pneumogastric nerves; and by exclusion, he located it in the general system. In a series of experiments (Flint, 1861) the following facts, some of which had been previously noted, were observed:

The chest was opened in a living animal, artificial respiration was carefully performed, inflating the lungs sufficiently but cautiously and taking care to change the air in the bellows every few moments. So long as this was continued, the animal made no respiratory effort; showing that for the time the respiratory sense was abolished. This was little more than a repetition of the classical experiment of Robert Hook, an account of which was published in 1664.

When the artificial respiration was interrupted, the respiratory muscles were thrown into contraction, and the animal made regular, and at last violent efforts. An artery was then opened and the color of the blood was noted. It was observed that the respiratory efforts began only when the blood in the vessel became dark. When artificial respiration was resumed, the respiratory efforts ceased only when the blood became red in the arteries.

While artificial respiration was being regularly performed, a large artery was opened and the system was drained of blood. When the hæmorrhage had proceeded to a certain extent, the animal made respiratory efforts, which became more and more violent, until they terminated, just before death, in general convulsions.

These facts, which may be successively observed in a single experiment, remained precisely the same when both pneumogastric nerves had been divided in the neck.

The conclusion which may legitimately be drawn from the above-mentioned facts is that the respiratory sense does not always and necessarily originate in the lungs, for it operates when the lungs are regularly filled with pure air, if the system be drained of the oxygen-carrying fluid.

A similar conclusion was arrived at by Rosenthal (1862) and by Pflüger (1868). Pflüger produced asphyxia in dogs by causing them to respire pure nitrogen. In his experiments, he analyzed the blood after thirty seconds and after one minute of inhalation of nitrogen. He found a great diminution in oxygen with very slight increase in carbon dioxide at the end of thirty seconds. After one minute the oxygen was reduced from 14·35 per cent. in volume to 0·2 per cent., and the carbon dioxide from 36·9 to 29·9. As a conclusion he stated that "no one, therefore, can be of the opinion that dyspnœa and asphyxia in breathing indifferent gases are connected with the accumulation of carbon dioxide."

In 1877 the experiments made in 1861 were repeated and extended (Flint). The later experiments were made upon dogs, in the following way: The animals were brought under the influence of ether, the chest was opened and artificial respiration was carried on by means of a bellows fixed in the trachea. The great vessels given off from the arch of the aorta were isolated so that they could be separately constricted at will. In a number of experiments upon different animals, the innominate artery and the left subclavian were constricted, and the animal began to make respiratory efforts about two minutes after, although artificial respiration was kept up constantly and efficiently. The animals made no respiratory efforts when the vessels given off from the arch of the aorta were left free and when the aorta was tied in the chest, which cut off the supply of blood from the trunk and the lower extremities. In the experiments in which the vessels going to the head and upper extremities were constricted, the respiratory efforts always ceased when the vessels were freed.

The object of these experiments was to study the effects of cutting off the supply of oxygenated blood from different parts. It may be assumed that the respiratory nervous centre is in the medulla oblongata, and an attempt was made to devise some means of cutting off the arterial supply from this part. Animals respire when all of the encephalic centres have been destroyed except the medulla oblongata, so that it is improbable that cutting off the supply of blood from the brain would affect the muscles of respiration, provided that artificial respiration were efficiently maintained. Blood may be supplied to the medulla oblongata by the internal carotids, which are connected with the circle of Willis, by the vertebral arteries, which unite to form the basilar artery, and perhaps by other vessels; but it is certain that if all the arteries given off from the arch of the aorta be tied, the medulla must be deprived of oxygenated blood.

In one experiment, the innominate artery and the left subclavian artery were constricted, and the animal made respiratory efforts in two minutes and eight seconds, notwithstanding that artificial respiration was kept up.

In another experiment, the same vessels were constricted, and the animal made respiratory efforts in two minutes and five seconds.

In a third experiment, both subclavian arteries and both carotids were constricted, and the animal made respiratory efforts in two minutes and seven seconds. Both vertebral arteries and both carotids were constricted, and the animal made no respiratory efforts for five minutes; but respiratory efforts were made in one minute and thirty-five seconds after both subclavians had been constricted in addition to the vertebrals and carotids.

It seems from these experiments, that in order to induce respiratory efforts in an animal under the influence of ether and with the lungs supplied with air by artificial respiration, either the innominate artery and the left subclavian artery, or both subclavians, both carotids and both vertebral arteries, must be tied. In other words, according to the view taken of the cause of these respiratory efforts, the supply of blood to the medulla oblongata can not be cut off completely except by tying all the vessels given off from the arch of the aorta.

These observations, taken in connection with the experiments of 1861, lead to the conclusion that the sense of want of air, under certain conditions, is due to a want of circulation of oxygenated blood in the medulla oblongata. This view has been advanced by some writers, but it has lacked the positive experimental proof afforded by the experiments of 1877.

If the sense of want of air be regarded as due, under certain conditions, to a deficiency of oxygen in the medulla oblongata—which can hardly be doubted—it becomes an important question to determine whether the normal respiratory movements be actually reflex in their character or whether they be due to direct excitation of the nerve-cells in the respiratory centre.

It is difficult to account for the phenomena observed in experiments in which the pneumogastrics are divided or stimulated, without assuming that these nerves sometimes—and possibly always, in tranquil respiration—convey an impression to the respiratory nervous centre, which gives rise to the ordinary automatic and periodical action of the muscles of inspiration. If such an impression be conveyed from the lungs by the afferent fibres of the pneumogastrics, it could not operate when both pneumogastrics are divided in the neck. This operation, as is well known, profoundly affects the respiratory movements. After division of both nerves, the respirations become slow and unusually deep, without, as a rule, any evidence of respiratory distress. In dogs, the number of respirations often falls to four or five per minute, and their nervous mechanism seems to be modified. Any respiratory distress that occurs is due to the arrest of the respiratory movements of the larynx, and not to an exaggeration of the sense of want of air. When a feeble Faradic current is passed through the nerves, the respiratory movements are increased in frequency, but the movements are arrested by a relatively powerful current. This action is reflex.

In view of all the experimental facts bearing upon the question, it is probable that the respiratory movements are sometimes reflex and sometimes due to direct excitation of the cells of the respiratory centre by the absence of oxygen.

In perfectly normal and tranquil respiration, an impression is probably conveyed from the lungs to the respiratory centre by the pneumogastrics, which stimulates this centre to excite movements of inspiration. This is probably due to a gradual and progressive change in the character of the contents of the air-cells, although experiments are wanting to show the exact mechanism of this process.

When this reflex action is abolished, as by section of both pneumogastrics in the neck, the respiratory centre is stimulated only when the deficiency in the supply of oxygen becomes considerable. This excitation of the respiratory centre is direct. It requires a certain time for its operation, and this accounts for the slow respirations in animals after the pneumogastrics have been divided. Under certain physiological conditions, this direct stimulation may be added to the impression conveyed by the pneumogastrics, and it is probable that this always occurs in dyspnœa.

*Sense of Suffocation.*—The respiratory sense must not be confounded with the sense of distress from want of air, and its extreme degree, the sense of suffocation. The first is not a sensation, but an impression made upon the medulla oblongata, giving rise to involuntary respiratory movements. The necessities for oxygen on the part of the system regulate the supply of air to the lungs. Once in every seven or eight respirations, or when the respiratory movements are restricted under the influence of depressing emotions, an involuntary, deep or sighing inspiration is made, for the purpose of changing the air in the lungs more completely. The increased consumption of oxygen and a certain degree of interference with the mechanical process of respiration during violent muscular exercise put one "out of breath," and for a time the respiratory movements are exaggerated. This is perhaps the first physiological way in which the want of air is appreciated by the senses. A deficiency in hæmatosis, either from a vitiated atmosphere, mechanical obstruction in the air-passages or grave trouble in the general circulation, produces all grades of sensations, from the slight oppression which is felt in a crowded room, to the intense distress of suffocation. When hæmatosis is but slightly interfered with, only an indefinite sense of oppression is experienced, and the respiratory movements are a little increased, the most marked effect being an increase in the number and extent of sighing inspirations.

### Respiratory Efforts before Birth.

It is generally admitted that one of the most important uses of the placenta, and the one which is most immediately connected with the life of the fœtus, is a respiratory interchange of gases, analogous to that which takes place in the gills of aquatic animals. The placental villi are bathed in the blood of the uterine sinuses, and this is the only way in which the fœtal blood can receive oxygen. Legallois observed a bright-red color in the blood of the umbilical vein; and on alternately compressing and releasing the vessel, he saw the blood change in color successively from red to dark and from dark to red. Zweifel has demonstrated the presence of oxyhæmaglobine in the blood of the umbilical vessels by means of the spectroscope, thus showing that it contains oxygen. As oxygen is thus adequately supplied to the system, the fœtus is in a condition similar to that of the animals in which artificial respiration was effectually performed. The want of oxygen is fully met, and therefore no respiratory efforts take place. Respiratory movements will take place, however, even in very young animals, when there is a deficiency of oxygen in the system. It has been observed that the liquor amnii occasionally finds its way into the respiratory passages of the fœtus, where it could enter only during efforts at respiration. Winslow, in the latter part of the last century, first noticed respiratory efforts in the fœtuses of cats and dogs in the uterus of the mother during life; and many others have observed that when fœtuses are removed from vascular connection with the mother, they make vigorous efforts at respiration. After the death of the mother, the fœtus always makes a certain number of distinct and unmistakable respiratory efforts, which follow each other at regular intervals.

From what has been experimentally demonstrated with regard to the seat and cause of the respiratory sense after birth, it is evident that want of oxygen is the cause of respiratory movements in the fœtus. When the circulation in the maternal portion of the placenta is interrupted from any cause or when the blood of the fœtus is obstructed in its course to and from the placenta, the impression due to want of oxygen is made upon the medulla oblongata, and efforts at respiration are the result.

### Cutaneous Respiration.

Respiration by the skin, although very important in many of the lower orders of animals, is inconsiderable in the human subject and is even more insignificant in animals covered with hair or feathers; still, an appreciable quantity of oxygen is absorbed by the skin of the human subject, and a quantity of carbon dioxide, which is relatively larger, is exhaled. Exhalation of carbon dioxide, which is connected with the uses of the skin as a general eliminating organ and is by no means an essential part of the respiratory process, will be more fully considered in connection with the physiology of excretion. Carbon dioxide is given off with the general emanations from the surface, being found, also, in solution in the urine and in most of the secretions. It is well known that death follows the application of an impermeable coating to the entire cutaneous surface; but this is by no means due to a suppression of its respiratory office alone. The skin has other uses, particularly in connection with regulation of the animal temperature, which are much more important.

An estimate of the extent of the cutaneous, as compared with pulmonary respiration, has been made by Scharling, by comparing the relative quantities of carbon dioxide exhaled in the twenty-four hours. According to this observer, the skin performs $\frac{1}{60}$ to $\frac{1}{40}$ of the respiratory office. It is difficult to collect all the carbon dioxide given off by the skin under perfectly normal conditions. In the observations by Aubert, the estimate is very much lower than that given by Scharling.

### Asphyxia.

The effects of cutting off the supply of oxygen from the lungs are mainly referable to the circulatory system and have already been considered in treating of the influence of respiration upon the circulation. It will be remembered that in asphyxia the unaërated blood passes with so much difficulty through the systemic capillaries as finally to arrest the action of the heart. It is the experience of experimenters on living animals, that the movements of the heart, once arrested in this way, can not be restored; but that while the slightest regular movements continue, the heart's action will gradually return if air be re-admitted to the lungs.

A remarkable power of resisting asphyxia exists in newborn animals that have never breathed. This was noticed by Haller and others and has been the subject of many experiments. Legallois found that young rabbits would live for fifteen minutes deprived of air by submersion, but that this power of resistance diminished rapidly with age. W. F. Edwards has shown that there exists a great difference in this regard in different species. Dogs and cats, which are born with the eyes shut and in which there is at first a very slight development of animal heat, will show signs of life after submersion for more than half an hour; while Guinea-pigs, which are born with the eyes open, are much more active and produce a greater amount of heat, will not live for more than seven minutes. The explanation of this is that in most warm-blooded animals, during the very first periods of extraüterine life, the demands on the part of the system for oxygen are comparatively slight. At this time, there is very little activity in the general processes of nutrition and in the consumption of oxygen and the exhalation of carbon dioxide. The actual difference between the consumption of oxygen immediately after birth and at the age of a few days is sufficient to explain the remarkable power of resisting asphyxia just after birth.

*Breathing in a Confined Space.*—An important question connected with the physiology of asphyxia, is the effect on the system, of air vitiated by breathing in a confined space. There are here several points which present themselves for consideration. The effect of respiration on the air is to take away a certain proportion of oxygen and to add certain matters which are regarded as deleterious. The emanation which has been generally regarded as having the most decided influence upon the system is carbon dioxide; but this influence has been much over-estimated. In death from charcoal-fumes, it is generally carbon monoxide which is the poisonous agent. Regnault and Reiset exposed dogs and rabbits for many hours to an atmosphere containing twenty-three parts per hundred of carbon dioxide artificially introduced, and between thirty and forty parts of oxygen, without any ill effects. They took care, however, to keep up a free supply of oxygen.

These experiments are at variance with the result obtained by others, but Regnault and Reiset explained this difference by the supposition that the gases in other observations were probably impure, containing a little chlorine or carbon monoxide. This view is sustained by the experiments of Bernard with carbon monoxide. In animals killed by this gas, the blood, both venous and arterial, is of a bright-red color, which is due to the fixation of the gas by the blood-corpuscles. In this way, the red corpuscles, which act normally as respiratory agents, carrying oxygen to the tissues, are paralyzed, and the animal dies from asphyxia.

In breathing in a confined space, the distress and the fatal results are produced, in all probability, more by animal emanations and a deficiency of oxygen than by the presence of carbon dioxide. When the latter gas is removed as fast as it is produced, the effects of diminution in the proportion of oxygen are soon very marked, and they progressively increase until death occurs. The influence of emanations from the lungs and general surface is undoubtedly very considerable; and this fact, which almost all have experienced more or less, has been fully illustrated in several instances of large numbers of persons confined without proper change of air. Overcrowding is one of the most prolific sources of disease among the poorer classes of society; and there are many forms of disease prevalent in large cities, that are almost unknown in the rural districts and that can be alleviated only by proper sanitary regulations, which, unfortunately, it is often difficult to enforce.

In crowded assemblages, the slight diminution of oxygen, the elevation of temperature, increase in moisture, and particularly the presence of organic emanations, combine to produce unpleasant sensations. The effects of this carried to an extreme degree were exemplified in the confinement of the one hundred and forty-six English prisoners, for eight hours only, in the "Black Hole" of Calcutta, a chamber eighteen feet (5·486 metres) square, with only two small windows, and those obstructed by a veranda. Out of this number, ninety-six died in six hours, and one hundred and twenty-three, at the end of the eight hours. Many of those who immediately survived died afterward of putrid fever ("Annual Register," 1758). The incident of the "Black Hole of Calcutta" has frequently been repeated on emigrant and slave ships, by confining great numbers in the hold of the vessel, where they were entirely shut out from the fresh air.

The condition of the system has a marked and important influence on the rapidity with which the effects of vitiated atmosphere are manifested. As a rule, the immediate effects of confined air are not developed so soon in weak and debilitated persons as in those who are active and powerful. It has sometimes been observed, in cases where a male and female have attempted suicide together by the fumes of charcoal, that the female has been restored some time after life had become extinct in the male. This is probably owing to the greater demand for oxygen on the part of the male.

When poisoning by confined air is gradual, the system becomes accustomed to the toxic influence, the temperature of the body is lowered, and an animal will live in an atmosphere which will produce instantaneous death in one that is fresh and vigorous. Bernard has made a number of experiments on this point. In one of them, a sparrow was confined under a bell-glass for an hour and a half, at the end of which time another was introduced, the first being still quite vigorous. The second became instantly much distressed and died in five minutes; but ten minutes after, the sparrow which had been confined for more than an hour and a half was released and flew away.

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# CHAPTER VI.

## *ALIMENTATION.*

General considerations—Hunger—Seat of the sense of hunger—Thirst—Seat of the sense of thirst—Duration of life in inanition—Classification of alimentary substances—Nitrogenized alimentary substances—Non-nitrogenized alimentary substances—Inorganic alimentary substances—Alcohol—Coffee—Tea—Chocolate—Condiments and flavoring articles—Quantity and variety of food necessary to nutrition—Necessity of a varied diet.

In the organism of animals, every part is continually undergoing what may be called physiological wear; the nitrogenized constituents of the body are being constantly transformed into effete matter; and as these constituents never exist without inorganic matters, with which they are closely and inseparably united, it is found that the products of their disassimilation are always discharged from the body in combination with inorganic substances. This process of molecular change is a necessary condition of life. Its activity may be increased or retarded by various means, but it can not be arrested. The excrementitious matters which are thus formed are produced constantly by the tissues and must be continually removed from the organism.

It is evident, from the amount of matter that is daily discharged from the body, that the process of disassimilation must be very active. Its constant operation necessitates a constant appropriation of new matter by the parts, in order that they may maintain their integrity of composition and be always ready to perform their offices in the economy. The blood contains all the materials necessary for the regeneration of the organism. Its inorganic constituents are found generally in the form in which they exist in the substance of the tissues; but the organic constituents of the parts are formed in the substance of the tissues themselves, by a transformation of matters furnished by the blood. The physiological wear of the organism is, therefore, being constantly repaired by the blood; but in order to keep the great nutritive fluid from becoming impoverished, the matters which it is constantly losing must be supplied from some source out of the body, and this necessitates the ingestion of articles which are known as food. Food is taken into the body in obedience to a want on the part of the system, which is expressed by the sensation of hunger, when it relates to solid or semi-solid matters, and of thirst, when it relates to water.

## Hunger and Thirst.

The term hunger may be applied to all degrees of that peculiar want felt by the system, which leads to the ingestion of nutritive substances. Its first manifestations are, perhaps, best expressed by the term appetite; a sensation by no means disagreeable, and one which may be excited by the sight, smell, or even the recollection of savory articles, at times when it does not absolutely depend on a want in the system. In the ordinary and moderate development of the appetite, it is impossible to say that the sensation is referable to any distinct part or organ. It is influenced in some degree by habit; in many persons, the feeling being experienced at or near the hours when food is ordinarily taken. If not soon gratified, the appetite is rapidly intensified until it becomes actual hunger. Except when the quantity of food taken is unnecessarily large, the appetite simply disappears on the introduction of food into the stomach and gives place to the sense of satisfaction which accompanies the undisturbed and normal action of the digestive organs; or in those who are in the habit of engaging in absorbing occupations at that time, the only change experienced is the absence of desire for food.

It has been observed that children and old persons do not endure deprivation of food so well as adults. This was noted in the case of the wreck of the frigate Medusa. After the wreck, one hundred and fifty persons, of all ages, were exposed on a raft for thirteen days, with hardly any food. Out of this number only fifteen survived; and the children, the young persons and the aged, were the first to succumb.

Important modifications in the appetite are due to temperature. In cold climates and during the winter season in all climates, the desire for food is notably increased, and the tastes are somewhat modified. Animal food, and particularly fats, are more agreeable at that time, and the quantity of nutriment which is demanded by the system is then considerably increased. In many persons the difference in the appetite in warm and cold seasons is very marked.

Exercise and occupation, both mental and physical, when not pushed to the point of exhaustion, increase the desire for food and undoubtedly facilitate digestion. Certain articles, especially the vegetable bitters, taken into the stomach immediately before the time when food is habitually taken, frequently have the same effect; while other articles which do not satisfy the requirements of the system have a tendency to diminish the desire for food. Many articles of the materia medica, especially preparations of opium, have, in some persons, a marked influence in diminishing the appetite. The abuse of alcoholic stimulants will sometimes take away all desire for food. When hunger is pressing, it has been observed that tobacco, in those who are accustomed to its use, will frequently allay the sensation for a time.

If food be not taken in obedience to the demands of the system as expressed by the appetite, the sensation of hunger becomes most distressing. It is then manifested by a peculiar and indescribable sensation in the stomach, which soon becomes developed into actual pain. This is generally accompanied with intense pain in the head and a feeling of general distress, which soon render the satisfaction of this imperative demand on the part of the system the absorbing idea of existence. Furious delirium frequently supervenes after a few days of complete abstinence; and this is generally the immediate precursor of death. It is unnecessary to cite the many instances in which murder and cannibalism have been resorted to when starvation is imminent; suffice it to say, that the extremity of hunger or of thirst, like the sense of impending suffocation, is a demand on the part of the system so imperative, that it must be satisfied if within the range of possibility.

The question of the seat of the sense of hunger is one of considerable physiological interest. Saying that it is instinctively referred to the stomach, is simply expressing the fact that the sensation is of a nature to demand the introduction of food in the usual way. When the system is suffering from defective nutrition, as after prolonged abstinence or during recovery from diseases which have been accompanied by a lack of assimilation, the mere filling of the stomach produces a sensation of repletion of this organ, but the sense of hunger is not relieved; but if, on the other hand, the nutrition be active and sufficient, the stomach is frequently entirely empty for a considerable time without the development of the sense of hunger. The appetite is preserved and hunger is felt by persons who suffer from extensive organic disease of the stomach, and the sensation has been occasionally relieved by nutritious enemata or by injections into the veins. It is certain that the appetite and the sense of hunger are expressions of a want on the part of the organism, referred by the sensations to the stomach, but really existing in the general system. This can be completely satisfied only by the absorption of digested alimentary matters by the blood and their assimilation by the tissues.

The sense of hunger is undoubtedly appreciated by the cerebrum, and it has been a question whether there be any special nerves which convey this impression to the encephalon. The nerve which would naturally be supposed to have this office is the pneumogastric; but notwithstanding certain observations to the contrary, it has been shown that section of both of these nerves by no means abolishes the desire for food. Longet has observed that dogs eat, apparently with satisfaction, after section of the glosso-pharyngeal and lingual nerves. This observer is of the opinion that the sensation of hunger is conveyed to the brain through the sympathetic system. Although there are various considerations which render this somewhat probable, it is not apparent how it could be demonstrated experimentally. It is undoubtedly the sympathetic system of nerves which presides specially over nutrition; and hunger, which depends upon deficiency of nutrition, is certainly not conveyed to the brain by any of the cerebro-spinal nerves.

Thirst is the peculiar sensation which leads to the ingestion of water. In its moderate development, this is usually an indefinite feeling, accompanied by more or less sense of dryness and heat of the throat and fauces, and sometimes, after the ingestion of a quantity of very dry food, by a sensation referred to the stomach. When the sensation of thirst has become intense, the immediate satisfaction which follows the ingestion of a liquid, particularly water, is very great. Thirst is very much under the influence of habit; some persons experiencing a desire to take liquids only two or three times daily, while others do so much more frequently. The sensation is also sensibly influenced by the condition of the atmosphere as regards moisture, by exercise and by other conditions which influence the discharge of water from the body, particularly by the skin. A copious loss of blood is always followed by great thirst. This is frequently noticed in the inferior animals. After an operation involving hæmorrhage, they nearly always drink with avidity as soon as released. In diseases which are characterized by increased discharge of liquids, thirst is generally excessive.

The demand on the part of the system for water is much more imperative than for solids; in this respect being second only to the demand for oxygen. Animals will live much longer when deprived of solid food but allowed to drink freely than if deprived of both food and drink. A man, supplied with dry food but deprived of water, will not survive more than a few days. Water is necessary to the processes of nutrition, and acts, moreover, as a solvent in removing from the system the products of disassimilation.

After deprivation of water for a considerable time, the intense thirst becomes most distressing. The dryness and heat of the throat and fauces are increased and accompanied with a sense of constriction. A general febrile condition supervenes, the blood is diminished in quantity and becomes thickened, the urine is scanty and scalding, and there seems to be a condition of the principal viscera approaching inflammation. Death takes place in a few days, generally preceded by delirium.

The sensation of thirst is instinctively referred to the mouth, throat and fauces; but it is not necessarily appeased by the passage of water over these parts, and it may be effectually relieved by the introduction of water into the system by other channels, as by injecting it into the veins. Bernard has demonstrated, by the following experiment, that water must be absorbed before the demands of the system can be satisfied: He made an opening into the œsophagus of a horse, tied the lower portion, and allowed the animal to drink after he had been deprived of water for a number of hours. The animal drank an immense quantity, but the water did not pass into the stomach and the thirst was not relieved. He modified this experiment by causing dogs to drink, with a fistulous opening into the stomach by which the water was immediately discharged. They continued to drink without being satisfied, until the fistula was closed and the water could be absorbed.

In a case reported by Gairdner (1820), in the human subject, all the liquids swallowed passed out at a wound in the neck, by which the œsophagus had been cut across. The thirst in this case was insatiable, although buckets of water were taken in the day; but on injecting water, mixed with a little spirit, into the stomach, the sensation was soon relieved.

Although the sensation of thirst is referred to special parts, it is an expression of the want of liquids in the system and is to be effectually relieved only by their absorption by the blood. There are no nerves belonging to the cerebro-spinal system which have the office of conveying this sensation to the brain, division of which will abolish the desire for liquids. Experiments show that no effectual relief of the sensation is afforded by simply moistening the parts to which the heat and dryness are referred. As a demand on the part of the system, it is entirely analogous to the sense of want of air and of hunger, differing only in the way in which it is manifested.

The length of time that life continues after complete deprivation of food and drink is very variable. The influences of age and obesity have already been referred to. Without citing the individual instances of starvation in the human subject which have been reported, it may be stated, in general terms, that death occurs within five to eight days after total deprivation of food. In the instance of the one hundred and fifty persons, wrecked on the frigate Medusa, in 1816, who were exposed on a raft in the open sea for thirteen days, only fifteen were found alive. Savigny, one of the survivors, gave, in an inaugural thesis, a very instructive and accurate account of this occurrence, which has been very generally quoted in works of physiology. Authentic instances are on record in which life has been prolonged much beyond the period above mentioned; but they generally occurred in persons who were so situated as not to suffer from cold, which the system, under this condition, has very little power to resist. In these cases, also, there was no muscular exertion, and water was generally taken in abundance.

Bérard quoted the example of a convict who died of starvation after sixty-three days, but in this case water was taken. An instance of eight miners who survived after five days and sixteen hours of almost complete deprivation of food is referred to in works upon physiology. Bérard has also quoted, from various authors, instances of deprivation of food for periods varying between four months and sixteen years; but these accounts are not properly authenticated and are discredited by physiologists. They generally occurred in hysterical females, and their consideration belongs to psychology rather than to physiology. According to Chossat, death from starvation occurs after a loss of four-tenths of the weight of the body, the time of death being variable in different classes of animals.

Thirty to thirty-five days may be taken as the average duration of life in dogs deprived entirely of food and drink. It is important to bear in mind this fact in connection with observations on the nutritive value of different articles of food.

## ALIMENTATION.

Under the name of aliment, in its widest signification, it is proposed to include all articles composed of or containing substances in a form which enables them to be used for the nourishment of the body, either by being themselves appropriated by the organism, by influencing favorably the process of nutrition, or by retarding disassimilation. Those substances which are themselves appropriated may be called direct aliments; and those which simply assist nutrition without contributing reparative material, together with those which retard disassimilation, may be termed accessory aliments. In this definition of aliment, nothing is excluded which contributes to nutrition. The air must be considered in this light, as well as water and all articles which are commonly called drinks.

In the various articles used as food, nutritious substances are frequently combined with each other and with indigestible and innutritious matters. The constituents of the food which are directly used in nutrition are the true alimentary substances, embracing, thus, only those which are capable of absorption and assimilation. The ordinary food of the warm-blooded animals contains alimentary matters united with innutritious substances from which they are separated in digestion. This necessitates a complicated digestive apparatus. In some of the inferior animals, the quantity of nutritious matter forms so small a part of the ingesta that the digestive apparatus is even more complicated than in the human subject. This is specially marked in the herbivora, the flesh of which forms an important part of the diet of man. In addition to what are distinctly recognized as alimentary substances, food has many constituents which exert an important influence on nutrition, which have never been isolated and analyzed, but which render it agreeable. Many of these are developed in the process of cooking.

Alimentary substances belong to the inorganic, vegetable, and animal kingdoms. They are generally divided into the following classes:

1. Organic nitrogenized substances (albumen, fibrin, caseine, myosine etc.), belonging to the animal kingdom, and vegetable nitrogenized substances, such as gluten and legumine.

2. Organic nitrogenized substances (sugars, starch and fats).

3. Inorganic substances.

*Nitrogenized Alimentary Substances.*—In the nutrition of certain classes of animals, these substances are derived exclusively from the animal kingdom, and in others, exclusively from the vegetable kingdom; but in man, both animals and vegetables contribute nitrogenized matters. In both animal and vegetable food, nitrogenized substances are always found combined with inorganic matters (water, sodium chloride, the phosphates, sulphates etc.), and frequently with non-nitrogenized matters, especially the carbohydrates.

The most important nitrogenized alimentary constituents of food are contained in the muscular substance, eggs, milk, the juices of vegetables, cereal grains etc. Many of these substances have been isolated and studied by chemists. Among the most important are myosine, the chief organic constituent of muscle, the various albumens found in eggs and in animal fluids, analogous substances existing in vegetables, caseine in milk, a substance sometimes called vegetable caseine, vitelline in yelk of egg, fibrin, gelatine, and gluten, an important alimentary substance found in the cereal grains, etc. A distinctive character of these substances is that they all contain nitrogen, being composed of carbon, oxygen, hydrogen and nitrogen, with probably a small quantity of sulphur. They are all either liquid or semi-solid in consistence, not crystallizable, and are coagulable by various reagents. The type of substances of this class is albumen, which has the provisional formula $C_{72}H_{112}O_{22}N_{18}S$ (Lieberkühn); and they are sometimes called albuminoids. They are also called proteids, after a hypothetical substance described by Mulder, under the name of proteine.

The nitrogenized substances are found in animal bodies, as has already been stated. They originate in vegetables by a union of nitrogen, derived from saline matters, with the carbohydrates, the carbohydrates in vegetables being produced from carbonic acid and water. No part of the nitrogen used by vegetables in the formation of the albuminoids is derived from the atmosphere (Hoppe-Seyler).

A distinctive character of substances of this class is that under favorable conditions of heat and moisture they undergo a peculiar form of decomposition, called putrefaction. In the process of digestion, these substances are changed into peptones, and afterward, it is thought, into leucine, tyrosine and some other substances not well defined. An analogous decomposition is said to take place under the influence of dilute hydrochloric acid, at a temperature of 104° Fahr. (40° C.), and of dilute sulphuric acid, at a temperature of 212° Fahr. (100° C.). The chemical history of these substances would require for its comprehension an elaborate description such as properly belongs only to special works on physiological chemistry.

*Non-Nitrogenized Alimentary Substances.*—The important non-nitrogenized alimentary substances are sugars, starch and fats. They are all composed of carbon, hydrogen and oxygen. In sugars and starch, the hydrogen and oxygen exist in the proportion to form water, and these matters are therefore called carbohydrates. The non-nitrogenized constituents of food are of organic origin, definite chemical composition and crystallizable.

*Sugars.*—Many varieties of sugar occur in food, and this substance may be derived from both the animal and the vegetable kingdoms. The most common varieties derived from animals are sugar of milk, and honey, beside a small quantity of liver-sugar, which is taken whenever the liver is used as food. The sugars derived from the vegetable kingdom are cane-sugar, under which head may be classed all varieties of sugar except that obtained from fruits, and grape-sugar, which comprises all the varieties existing in fruits. The following are the formulæ for the different varieties of sugar in a crystalline form:

Cane-Sugar (Saccharose), $C_{22}H_{12}O_{11}$

Milk-Sugar (Lactose), $C_{12}H_{24}O_{12}$

Grape-Sugar (Glucose, Dextrose), $C_6H_{12}O_6$

All varieties of sugar have a peculiar, sweet taste; they are all soluble in water, glucose being more soluble than cane-sugar or lactose; glucose is sparingly soluble in alcohol, which dissolves small quantities, only, of cane-sugar or lactose; glucose ferments readily and is changed into alcohol and carbon dioxide; cane-sugar and lactose are said to be incapable of fermentation, but cane-sugar may easily be converted into fermentable glucose, and lactose, into a fermentable sugar called galactose, by boiling with dilute mineral acids; they are capable of being converted into lactic acid in the presence of decomposing nitrogenized matters; they are inflammable, leaving an abundant carbonaceous residue and giving off a peculiar odor of caramel; they undergo other modifications when treated with the mineral acids or with alkalies, which are interesting more in a chemical than a physiological point of view. Of all the varieties of sugar, that made from the sugar-cane is the most soluble, the sweetest and the most agreeable. Beet-root sugar is identical with cane-sugar.

Much of the sugar used in the nutrition of the organism is formed in the body by the digestion of starch. This transformation of starch may be effected artificially. The sugar thus formed, called glucose, is identical in composition with grape-sugar. Except in the milk during lactation, this is the only form in which sugar exists in the organism, all the sugar of the food being converted into glucose before it is taken into the blood.

*Starch.*—A non-nitrogenized substance, closely resembling sugar in its ultimate composition ($C_6H_{10}O_5$), is contained in abundance in a great number of vegetables. It is found particularly in the cereals (wheat, rye, corn, barley, rice and oats), in the potato, chestnuts, and in the grains of leguminous plants (beans, peas, lentils and kidney-beans), in the tuberous roots of the yam, tapioca and sweet-potato, in the roots of the *Maranta arundinacea* (arrowroot), in the sago-plant and in the bulbs of orchis. In the cereals, after desiccation, the proportion of starch is usually between sixty and seventy per cent. It is most abundant in rice, which contains, after desiccation, 88·65 per cent.

When extracted in a pure state, starch is in the form of granules, varying in size between $\frac{1}{10000}$ and $\frac{1}{400}$ of an inch (2·5 and 62·5 $\mu$), and presenting, in most varieties, certain peculiarities of form. The granule frequently is marked by a little conical excavation called the hilum, and the starch-substance is arranged in the form of concentric laminæ, the outlines of which are often quite distinct. When starch is rubbed between the fingers, these little, hard bodies give it rather a gritty feel and produce a crackling sound. The different varieties of starch may be recognized microscopically by the peculiar appearance of the granules.

Starch is insoluble in cold water; but when boiled with several times its volume of water, the granules swell up, become transparent, and finally fuse together, mingling with the water and giving it a mucilaginous consistence. The mixture on cooling forms a jelly-like mass of greater or less consistence. This change in starch is called hydration and is important as one of the transformations which take place in the process of digestion, when starch is taken uncooked. This change is generally effected more or less completely, however, in the process of cooking.

FIG. 49.—*Arrowroot starch-granules; magnified 370 diameters* (from a photograph taken at the United States Army Medical Museum).

The most important properties of starch are connected with its transformation, first into dextrine, and finally into glucose. This always takes place in digestion, before starch can be absorbed. In the digestive apparatus, the change into sugar is almost instantaneous, and the intermediate substance, dextrine, is not easily recognized. By boiling starch for a number of hours with dilute sulphuric acid, it is transformed, without any change in chemical composition, into dextrine, which is soluble. If the action be continued, it appropriates one atom of water and is converted into glucose. The change of starch into dextrine may be effected by a dry heat of about 400° Fahr. (204° C.), a process which is commonly employed in commerce.

*Vegetable Substances resembling Starch.*—In certain vegetables, substances isomeric with starch, but presenting slight differences as regards general properties and reactions, have been described, but they possess no great importance as alimentary matters and demand only a passing mention. These are inuline, lichenine, cellulose, pectose, mannite, mucilages and gums. Inuline is found in certain roots. It is convertible into sugar but does not pass through the intermediate stage of dextrine. It differs from starch in being very soluble in hot water. Lichenine is found in many kinds of edible mosses and lichens. It differs from starch only in its solubility. Mannite is a sweetish substance found in manna, mushrooms, celery, onions and asparagus. It is perhaps more analogous to sugar than to starch, but it is not fermentable and has no influence on polarized light.

Gums and mucilages may enter to a certain extent into the composition of food, but they can hardly be considered as alimentary matters. Gums are found exuding from certain trees, first in a fluid state, but becoming hard on exposure to the air. A viscid, stringy mucilage is found surrounding many grains, such as the flax-seed and quince-seeds, and exists in various roots and leaves. Both gums and mucilages mix readily with water, giving it a consistence called mucilaginous. The composition of gum is $C_{20}H_{10}O_{10}$. Experiments have shown that gum passes unchanged through the alimentary canal and has no nutritive properties. Gum is mentioned in this connection from the fact that it is frequently used in the treatment of disease and is thought by many to be nutritious.

The carbohydrates, although important articles of food and especially useful in the processes involved in the production of animal heat, are not in themselves capable of sustaining life.

*Fats.*—Fatty matters, derived from both the animal and the vegetable kingdoms, are important articles of food. As a constituent of the organism, fat is found in all parts of the body, with the exception of the bones, teeth and fibrous tissues. It necessarily constitutes an important part of all animal food and is taken in the form of adipose tissue, infiltrated in the various tissues in the form of globules and granules of oil, and in suspension in the caseine and water in milk. Animal fat is a mixture of oleine, palmitine and stearine, in various proportions, and possesses a consistence which depends upon the relative quantities of these substances.

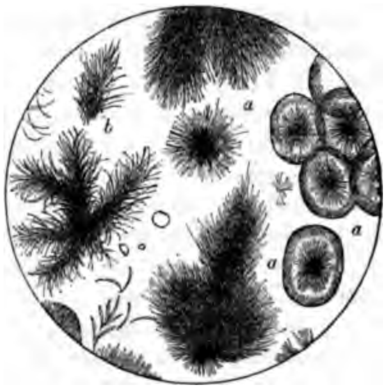


FIG. 50.—*Crystals of palmitine and palmitic acid* (Funke). *a, a, a*, palmitine; *b*, palmitic acid.

The different varieties of animal fats do not demand special consideration as articles of diet. Butter, an important article of food, is somewhat different from the fat extracted from adipose tissue, but most varieties of fat lose their individual peculiarities in the process of digestion and are apparently identical when they find their way into the lacteal vessels.

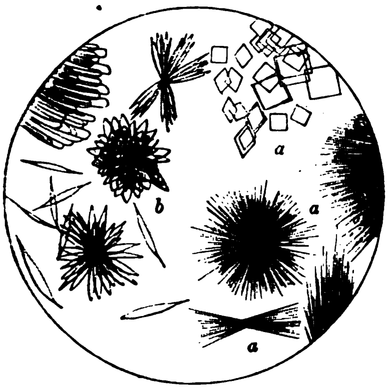


FIG. 51.—*Crystals of stearine and stearic acid* (Funke). *a, a, a*, stearine; *b*, stearic acid.

In the vegetable kingdom, fat is particularly abundant in seeds and grains, but it exists in quantity in some fruits, as in the olive. Here it is generally called oil. It exists in considerable proportion in nuts and in certain quantity in the cereals, particularly Indian corn.

Fat, both animal and vegetable, may be either liquid or solid. It has a peculiar oily feel, a neutral reaction, and is insoluble in water and soluble in alcohol—particularly hot alcohol—chloroform, ether, benzine and solutions of soaps. The solid varieties are exceedingly soluble in the oils. Treated with alkalies at a high temperature and in the presence of water, the fats are decomposed into fatty acids and glycerine, the acids uniting with the bases to form soaps. Alkaline, mucilaginous, and some animal fluids—particularly the pancreatic juice—are capable of holding fat in a state of minute and permanent subdivision and suspension, forming what are known as emulsions.

The three varieties of fats usually recognized are stearine and palmitine, which are solid at the temperature of the body, and oleine, which is liquid. The formulæ for these varieties are the following:

Stearine (Tristearine), $C_{57}H_{110}O_6$

Palmitine (Tripalmitine), $C_{51}H_{98}O_6$

Oleine (Trioleine), $C_{57}H_{104}O_6$

It is noticeable that in the composition of fats, the hydrogen and oxygen do not exist in the proportions to form water, as they do in the carbohydrates, and that they are relatively poor in oxygen. One variety of fat can not be converted into another by chemical manipulation.

As alimentary substances, fats are undoubtedly of great importance. They are supposed by many to be particularly concerned in the production of animal heat. It has been proved by repeated experiments that fat, as a single article of diet, is insufficient for the purposes of nutrition.

*Inorganic Alimentary Substances.*—It has been shown that all the organs, tissues and fluids of the body contain inorganic matter in greater or less abundance. The same is true of vegetable products. All the organic nitrogenized matters contain mineral substances which can not be separated without incineration. When new organic matter is appropriated by the tissues to supply the place of that which has become effete, the mineral substances are deposited with them; and the organic matters, as they are transformed into excrementitious substances and discharged from the body, are always thrown off in connection with the mineral substances which enter into their composition. This constant discharge of inorganic matters, forming, as they do, an essential part of the organism, necessitates their introduction with the food, in order to maintain the normal constitution of the parts. As these matters are necessary to the proper constitution of the body, they must be regarded as alimentary substances.

*Water.*—This is one of the most important of the constituents of the organism, is found in every tissue and part without exception, is introduced with all kinds of food and is the basis of almost all drinks. As a rule it is taken in greater or less quantity in a nearly pure state. Although, as a drink, water should be colorless, odorless and tasteless, it always contains more or less saline and other matters in solution, with a certain quantity of air. The air and gases may be driven off by boiling or by removing the atmospheric pressure. The demand on the part of the system for water is regulated, to a certain extent, by the quantity discharged from the organism, and this is subject to great variations. The quantity taken as drink also depends very much on the constitution of the food as regards the water which enters into its composition.

*Sodium Chloride.*—Of all saline substances, sodium chloride is the one most widely distributed in the animal and the vegetable kingdoms. It exists in all varieties of food; but the quantity which is taken in combination with other matters is usually insufficient for the purposes of the economy, and common salt is generally added to certain articles of food, as a condiment, when it improves their flavor, promotes the secretion of certain of the digestive fluids and meets a nutritive demand on the part of the system. Experiments and observations have shown that a deficiency of sodium chloride in the food has an unfavorable influence on the general processes of nutrition.

*Calcium Phosphate.*—This is almost as common a constituent of vegetable and animal food as sodium chloride. It is seldom taken except in combination, particularly with nitrogenized alimentary matters. Its importance in alimentation has been experimentally demonstrated, it having been shown that in animals deprived as completely as possible of this salt, the nutrition of the body, particularly in parts which contain it in considerable quantity, as the bones, is seriously affected.

*Iron.*—Hæmaglobine, the coloring matter of the blood, contains, intimately united with organic matter, a certain proportion of iron. Examples of simple anæmia, which are frequently met with in practice and are almost always relieved in a short time by the administration of iron, are proof of the importance of this substance in alimentation. The quantity of iron which is discharged from the body is very slight, only a trace being discoverable in the urine. A small quantity of iron is frequently introduced in solution in the water taken as drink, and it is a constant constituent of milk and eggs. When its supply in the food is insufficient, it is necessary, in order to restore the normal processes of nutrition, to administer it in some form, until its proportion in the organism shall have reached the proper standard.

It is hardly necessary even to enumerate the other inorganic alimentary substances, as nearly all are in a state of such intimate combination with nitrogenized matters that they may be regarded as part of their substance. Suffice it to say, that all the inorganic matters which exist as constituents of the organism are found in the food. That these are essential to nutrition, can not be doubted; but it is evident that by themselves they are incapable of supporting life, as they can not be converted into either nitrogenized or non-nitrogenized organic matters.

*Alcohol.*—All distilled and fermented liquors and wines contain a greater or less proportion of alcohol. As these are so generally used as beverages, and as the effects of their excessive use are so serious, the influence of alcohol upon the organism has become one of the most important questions connected with alimentation. Some alcoholic beverages influence the functions solely through the alcohol which they contain; while others, as beer and porter, with a comparatively small proportion of alcohol, contain a considerable quantity of solid matter.

Alcohol ($C_2H_6O$), from its composition, is to be classed with the non-nitrogenized substances. It has already been stated that sugar and fat are essential to proper nutrition and that they undergo important changes in the organism. Alcohol is absorbed and taken into the blood; and it becomes a question of importance to determine whether it be consumed in the economy or whether it be discharged unchanged by the various emunctories.

Alcohol has long since been recognized in the expired air after it has been taken into the stomach; and late researches have confirmed the earlier observations with regard to its elimination in its original form, and have shown that after it has been taken in quantity, it exists in the blood and all the tissues and organs, particularly the liver and nervous system. Lallemand, Perrin and Duroy have stated, also, that there is a considerable elimination of alcohol by the lungs, skin and kidneys; but the accuracy of the experiments by which these results were arrived at has been questioned. The observations of Anstie and of Dupré have, indeed, thrown great doubt upon the chromic-acid test for alcohol, which was employed by the French observers above mentioned. Nevertheless, when alcohol has been taken in narcotic doses, there is some alcoholic elimination in the urine, as was shown long ago by Percy.

As the result of the final experiments of Anstie, it is certain that most of the alcohol which is taken in quantities not sufficient to produce alcoholic intoxication is consumed in the organism, and but a trivial quantity is thrown off, either in the urine, the fæces, the breath or the cutaneous transpiration. This question is of importance with regard to the moderate use of alcohol under normal conditions, and especially in its bearing upon the therapeutical action of the various alcoholic drinks administered in cases of disease.

Taken in moderate quantity, alcohol generally produces a certain degree of nervous exaltation which gradually passes off. In some individuals the mental faculties are sharpened by alcohol, while in others they are blunted. There is nothing, indeed, more variable than the immediate effects of alcohol on different persons. In large doses the effects are the well known phenomena of intoxication, delirum, more or less anæsthesia, coma, and sometimes, if the quantity be excessive, death. As a rule, the mental exaltation produced by alcohol is followed by reaction and depression, except in debilitated or exhausted conditions of the system, when the alcohol seems to supply a decided want.

The views of physiologists concerning the influence of a moderate quantity of alcohol on the nervous system are somewhat conflicting. That it may temporarily give tone and vigor to the system when the energies are unusually taxed, can not be doubted; but this effect is not produced in all individuals. The constant use of alcohol may create an apparent necessity for it, producing a condition of the system which must be regarded as pathological.

The immediate effects of the ingestion of a moderate quantity of alcohol, continued for a few days, are decided. It notably diminishes the exhalation of carbon dioxide and the discharge of other excrementitious matters, particularly urea. These facts have long since been experimentally demonstrated. Proper mental and physical exercise, tranquillity of the nervous system, and all conditions which favor the vigorous nutrition and development of the organism physiologically increase, rather than diminish, the quantity of the excretions, correspondingly increase the demand for food, and if continued, are of permanent benefit. Alcohol, on the other hand, diminishes the activity of nutrition. If its use be long continued, the assimilative powers of the system become so weakened that the proper quantity of food can not be appropriated, and alcohol is craved to supply a self-engendered want. The organism may, in many instances, be restored to its physiological condition by discontinuing the use of alcohol; but it is generally some time before the nutritive powers become active, and alcohol, meanwhile, seems absolutely necessary to existence.

Under ordinary conditions, when the organism can be adequately supplied with food, alcohol is undoubtedly injurious. When the quantity of food is insufficient, alcohol may supply the want for a time and temporarily restore the powers of the body; but the effects of its continued use, conjoined with insufficient nourishment, show that it can not take the place of other assimilable matters. These effects are too well known to the physician, particularly in hospital-practice, to need farther comment. Notwithstanding these undoubted physiological facts, alcohol, in some form, is used by almost every people on the face of the earth, civilized or savage. Whether this be in order to meet some want occasionally felt by and peculiar to the human organism, is a question upon which physiologists have found it impossible to agree. That alcohol, at certain times, taken in moderation, soothes and tranquillizes the nervous system and relieves exhaustion dependent upon unusually severe mental or physical exertion, can not be doubted. It is by far too material a view to take of existence, to suppose that the highest condition of man is that in which the functions, possessed in common with the lower animals, are most perfectly performed. Inasmuch as temporary insufficiency of food, great exhaustion of the nervous system, and various conditions in which alcohol seems to be useful, must of necessity often occur, it is hardly proper that this agent should be absolutely condemned; but it is the article, *par excellence*, which is liable to abuse, and the effects of which on the mind and body, when taken constantly in excess, are most serious.

Although alcohol imparts a certain warmth when the system is suffering from excessive cold, it is not proved that it enables men to endure a very low temperature for a great length of time. This end can be effectually attained only by an increased quantity of food. The testimony of Dr. Hayes, the Arctic explorer, is very strong upon this point. He says: " While fresh animal food, and especially fat, is absolutely essential to the inhabitants and travellers in Arctic countries, alcohol is, in almost any shape, not only completely useless but positively injurious .... Circumstances may occur under which its administration seems necessary; such, for instance, as great prostration from long-continued exposure and exertion, or from getting wet; but then it should be avoided, if possible, for the succeeding reaction is always to be dreaded; and, if a place of safety is not near at hand, the immediate danger is only temporarily guarded against, and becomes, finally, greatly augmented by reason of decreased vitality. If given at all, it should be in very small quantities frequently repeated, and continued until a place of safety is reached. I have known the most unpleasant consequences to result from the injudicious use of whiskey for the purpose of temporary stimulation, and have also known strong able-bodied men to have become utterly incapable of resisting cold in consequence of the long-continued use of alcoholic drinks." In a recent paper by General Greely (1887), is the following, which confirms the results of the experience of Hayes: "It seems to me to follow from these Arctic experiences that the regular use of spirits, even in moderation, under conditions of great physical hardship, continued and exhausting labor, or exposure to severe cold can not be too strongly deprecated, and that when used as a mental stimulus or as a physical luxury they should be taken in moderation. When habit or inclination induces the use of alcohol in the field, under conditions noted above, it should be taken only after the day's work is done, as a momentary stimulus while waiting for the preferable hot tea and food; or better, after the food, when going to bed, for then it may quickly induce sleep and its reaction pass unfelt."

It is not demonstrated that alcohol increases the capacity to endure severe and protracted bodily exertion. Its influence as a therapeutic agent, in promoting assimilation in certain conditions of defective nutrition, in relieving shock and nervous exhaustion, in sustaining the powers of life in acute diseases characterized by rapid emaciation and abnormally active disassimilation, etc., can hardly be doubted; but the consideration of these questions does not belong to physiology.

*Coffee.*—Coffee is an article consumed daily by many millions of human beings in all quarters of the globe. In armies it has been found almost indispensable, enabling men on moderate rations to perform an amount of labor which would otherwise be impossible. After exhausting efforts of any kind, there is no article which relieves the overpowering sense of fatigue so completely as coffee. Army-surgeons say that at night, after a severe march, the first desire of the soldier is for coffee, hot or cold, with or without sugar, the only essential being a sufficient quantity of the pure article. Almost every one can bear testimony from personal experience to the effects of coffee in relieving the sense of fatigue after mental or bodily exertion and in increasing the capacity for labor, especially mental work, by producing wakefulness and clearness of intellect. From these facts, the importance of coffee, either as an alimentary substance or as taking the place, to a certain extent, of aliment, is apparent.

Except in persons who, from idiosyncrasy, are unpleasantly affected by it, coffee, taken in moderate quantity and at proper times, produces an agreeable sense of tranquillity and comfort, with, however, no disinclination to exertion, either mental or physical. Its immediate influence upon the system, which is undoubtedly stimulant, is peculiar and is not followed by reaction or unpleasant after-effects. Habitual use renders coffee almost a necessity, even in those who are otherwise well nourished and subjected to no extraordinary mental or bodily strain. Taken in excessive quantity, or in those unaccustomed to its use, particularly when taken at night, it produces persistent wakefulness. These effects are so well known that it is often taken for the purpose of preventing sleep.

Experimental researches have shown that the use of coffee permits a reduction in the quantity of food, in workingmen especially, much below the standard which would otherwise be necessary to maintain the organism in proper condition. In the observations of De Gasparin upon the regimen of the Belgian miners, it was found that the addition of a quantity of coffee to the daily ration enabled them to perform their arduous labors on a diet which was even below that found necessary in prisons where this article was not used. Experiments have shown, also, that coffee diminishes the absolute quantity of urea discharged by the kidneys. In this respect, as far as has been ascertained, the action of coffee is like that of alcohol, and it may reasonably be supposed to retard disassimilation, with the important difference that it is followed by no unfavorable after-effects and can be used in moderation for an indefinite time with advantage.

A study of the composition of coffee shows a considerable proportion of what must be considered as alimentary matter. The following is the result of analyses by Payen:

| | |
|---|---|
| Cellulose | 34·000 |
| Water (hygroscopic) | 12·000 |
| Fatty substances | 10 to 13·000 |
| Glucose, dextrine, indeterminate vegetable acid | 15·500 |
| Legumine, caseine etc. | 10·000 |
| Potassium chlorolignate and caffeine | 3·5 to 5·000 |
| Nitrogenized organic matter | 3·000 |
| Free caffeine | 0·800 |
| Concrete, insoluble essential oil | 0·001 |
| Aromatic essence, of agreeable odor, soluble in water | 0·002 |
| Mineral substances; potash, magnesia, lime, phosphoric, silicic, and sulphuric acid and chlorine | 6·697 |
| | 100·000 |

The above is the composition of raw coffee, but the berry is seldom used in that form, being usually subjected to roasting before an infusion is made. During this process, the grains are considerably swollen, but they lose sixteen or seventeen per cent. in weight. A peculiar, aromatic substance is also developed by roasting. If the torrefaction be pushed too far, much of the agreeable flavor of coffee is lost, and an acrid, empyreumatic substance is produced.

*Tea.*—An infusion of the dried and prepared leaves of the tea-plant is perhaps as common a beverage as coffee, and taking into consideration its large consumption in China and Japan, it is actually used by a greater number of persons. Its effects upon the system are similar to those of coffee, but they are generally not so marked. Ordinary tea, taken in moderate quantity, like coffee, relieves fatigue and increases mental activity, but does not usually produce such persistent wakefulness.

It is unnecessary to describe all the varieties of tea in common use. There are, however, certain varieties, called green teas, which present important differences, as regards composition and physiological effects, from the black teas, which latter are more commonly used. The following is a comparative analysis of these two varieties by Mulder:

| CONSTITUENTS. | CHINESE TEA. | | JAVANESE TEA. | |
|---|---|---|---|---|
| | Green. | Black. | Green. | Black. |
| Volatile oil | 0·79 | 0·60 | 0·98 | 0·65 |
| Chlorophyl | 2·22 | 1·84 | 3·24 | 1·28 |
| Wax | 0·28 | .... | 0·32 | .... |
| Resin | 2·22 | 3·64 | 1·64 | 2·44 |
| Gum | 8·56 | 7·28 | 12·20 | 11·08 |
| Tannin | 17·80 | 12·88 | 17·56 | 14·80 |
| Theine | 0·43 | 0·46 | 0·60 | 0·65 |
| Extractive | 22·80 | 19·88 | 21·68 | 18·64 |
| Apotheme | .... | 1·48 | .... | 1·64 |
| Extract obtained by hydrochloric acid | 23·60 | 19·12 | 20·36 | 18·24 |
| Albumen | 3·00 | 2·80 | 3·64 | 1·28 |
| Fibrous matter | 17·08 | 28·32 | 18·20 | 27·00 |
| | 98·78 | 98·30 | 100·42 | 97·70 |
| Salts included in the above | 5·56 | 5·24 | 4·76 | 5·36 |

Both tea and coffee contain peculiar organic substances. The active principle of tea is called theine, and the active principle of coffee, caffeine. As they are supposed to be particularly efficient in producing the peculiar effects upon the nervous system which are characteristic of both tea and coffee, there is good reason to suppose that they are nearly identical in their physiological effects. Analyses more recent than the one quoted from Mulder (Stenhouse, Peligot) have shown that theine, or caffeine ($C_8H_{10}N_4O_2 + H_2O$), exists in greater proportion in tea than in coffee; but as a rule, a greater quantity of soluble matter is extracted in the preparation of coffee, which may account for its more marked effects upon the system. Some analyses have given as much as six per cent. as the proportion of theine in tea (Landois).

*Chocolate.*—Chocolate is made from the seeds of the cocoa-tree, roasted, deprived of their husks, and ground with warm rollers into a pasty mass with sugar, flavoring substances being sometimes added. It is then made into cakes, cut into small pieces or scraped to a powder, and boiled with milk or milk and water, when it forms a thick, gruel-like drink, which is highly nutritive and has some of the exhilarating properties of coffee or tea. Beside containing a large proportion of nitrogenized matter resembling albumen, the cocoa-seed is particularly rich in fatty matter, and contains a peculiar substance, theobromine ($C_7H_8N_4O_2$), analogous to caffeine and theine, which is supposed to possess similar physiological properties.

The following is an analysis by Payen of the cocoa-seeds freed from the husks but not roasted. Torrefaction has the effect of developing the peculiar aromatic principle, and of moderating the bitterness, which is always more or less marked:

| | | |
|---|---|---|
| Fatty matter (cocoa-butter) | 48 to 50 | |
| Albumen, fibrin and other nitrogenized matter | 21 " | 20 |
| Theobromine | 4 " | 2 |
| Starch (with traces of saccharine matter) | 11 " | 10 |
| Cellulose | 3 " | 2 |
| Coloring matter, aromatic essence | Traces. | |
| Mineral substances | 3 to | 4 |
| Hygroscopic water | 10 " | 12 |
| | 100 | 100 |

It is evident, from the above table, that cocoa with milk and sugar, the ordinary form in which chocolate is taken, must form a very nutritious mixture. Its influence as a stimulant, supplying the place of matter which is directly assimilated, and retarding disassimilation, is dependent, if it exist at all, upon the theobromine; but its stimulating properties are slight as compared with those of coffee and tea.

*Condiments and Flavoring Articles.*—The refinements of cookery involve the use of many articles which can not be classed as alimentary substances. Pepper, capsicum, vinegar, mustard, spices and other articles of this class, which are so commonly used in various sauces, have no decided influence on nutrition, except in so far as they promote the secretion of the digestive fluids. Common salt, however, is very important, and this has been considered in connection with inorganic alimentary substances. The various flavoring seeds and leaves, truffles, mushrooms etc. have no physiological importance except as they render articles of food more palatable.

*Quantity and Variety of Food necessary to Nutrition.*—The inferior animals, especially those not subjected to the influence of man, regulate by instinct the quantity and kind of food which they consume. The same is true of man during the earliest periods of his existence; but later in life, the diet is variously modified by taste, habit, climate, and what may be termed artificial wants. It is usually a safe rule to follow the appetite with regard to quantity, and the tastes, when they are not manifestly vitiated or morbid, with regard to variety. The cravings of nature indicate when to change the form in which nutriment is taken; and that a sufficient quantity has been taken is manifested by a sense, not exactly of satiety, but of evident satisfaction of the demands of the system. During the first periods of life, the supply must be a little in excess of the actual loss, in order to furnish materials for growth; during the later periods, the quantity of nitrogenized matter assimilated is somewhat less than the loss; but in adult age, the system is maintained at a tolerably definite standard by the assimilation of matter about equal in quantity to that which is discharged in the form of excretions.

Although the loss of substance by disassimilation creates and regulates the demand for food, it is an important fact, never to be lost sight of, that the supply of food has a very great influence upon the quantity of the excretions. An illustration of this is the influence of food upon the exhalation of carbon dioxide; and this is but an example of what takes place with regard to other excretions. The quantity of the excretions is even more strikingly modified by exercise, which, within physiological limits, increases the vigor of the system, provided the increased quantity of food required be supplied.

While a certain amount of waste of the system is inevitable, it is a conservative provision, that when the supply of new material is diminished, life is preserved—not, indeed, in all its vigor—by a corresponding reduction in the quantity of excretions; and in the same way, the forces are retained after complete deprivation of food much longer than if disassimilation proceeded always with the same activity.

As regards the quantity of food necessary to maintain the system in proper condition, it is evident that this must be greatly modified by habit, climate, the condition of the muscular system, age, sex etc., as well as by idiosyncrasies.

The daily loss of substance which must be supplied by matters introduced from without is very great. A large portion of this discharge takes place by the lungs, and a consideration of the mode of introduction of gases to supply part of this waste belongs to the subject of respiration. The most abundant discharge which is compensated by absorption from the alimentary canal is that of water, both in a liquid and vaporous condition. The entire quantity of water daily removed from the system has been estimated at about four and a half pounds (2,041 grammes), and it is probable that about the same quantity is introduced in the form of drink and as a constituent of the so-called solid articles of food. The quantity which is taken in the form of drink varies with the character of the food. When the solid articles contain a large proportion of water, the quantity of drink may be diminished; and it is possible, by taking a large quantity of the watery vegetables, to exist entirely without drink. There is no article more frequently taken than water, merely as a matter of habit, any excess being readily removed by the kidneys, skin and lungs. Dalton estimates the daily quantity necessary for a full-grown, healthy male, at fifty-four fluid ounces (1,530 grammes), or 3·38 pounds.

The quantity of solid food necessary to the proper nourishment of the body is shown by estimating the solid matter in the excretions; and the facts thus ascertained correspond very closely with the quantity of material which the system has been found to actually demand. The estimates of Payen, the quantity of carbon and of nitrogenized matter in a dry state being given, are generally quoted and adopted in works on physiology. According to this observer, the following are the daily losses of the organism:

| | | |
|---|---|---|
| Carbon (or its equivalent). | Respiration, 8·825 oz. (250 grammes)<br>Excretions, 2·116 oz. ( 60 grammes) | 10·941 oz. (310 grammes). |
| Nitrogenized substances (containing 308·64 grains, or 20 grammes of nitrogen) | | 4·586 oz. (130 grammes). |
| | | 15·527 oz. (440 grammes). |

From this he estimates that the normal ration, supposing the food to consist of lean meat and bread, is as follows:

| | | |
|---|---|---|
| Bread | | 35·300 oz. (1,000 grammes). |
| Meat (without bones) | | 10·088 oz. (286 grammes). |
| | | 45·388 oz. (1,286 grammes). |
| | Nitrogenized substances. | Carbon. |
| Bread contains | 2·469 oz. (70·00 grammes) and | 10·582 oz. (300·00 grammes). |
| Meat contains | 2·125 oz. (60·26 grammes) and | 1·109 oz. (31·46 grammes). |
| | 4·594 oz. (130·26 grammes) and | 11·691 oz. (331·46 grammes). |

This daily ration, which is purely theoretical, is shown by actual observation to be nearly correct. Dalton says: "According to our own observations, a man in full health, taking active exercise in the open air, and restricted to a diet of bread, fresh meat, and butter, with water and coffee for drink, consumes the following quantities per day:

| | | |
|---|---|---|
| Meat | 453 grammes, or about | 16 oz. |
| Bread | 540 " " | 19 oz. |
| Butter or fat | 100 " " | 3·5 oz. |
| Water | 1,530 " " | 54 oz. |

Bearing in mind the great variations in the nutritive demands of the system in different persons, it may be stated, in general terms, that in an adult male, ten to twelve ounces (282 to 340 grammes) of carbon and four to five ounces (113 to 142 grammes) of nitrogenized matter, estimated dry, are discharged from the organism and must be replaced by the ingesta; and this demands a daily consumption of between two and three pounds (907 and 1,361 grammes) of solid food, the quantity of food depending, of course, greatly on its proportion of solid, nutritive constituents.

It is undoubtedly true that the daily ration has frequently been diminished considerably below the physiological standard, in charitable institutions, prisons etc.; but when there is complete inactivity of body and mind, this produces no other effect than that of slightly diminishing the weight and strength. The system then becomes reduced without any actual disease, and there is simply a diminished capacity for labor; but in the alimentation of large bodies of men subjected to exposure and frequently called upon to perform severe labor, the question of food is of great importance, and the men collectively are like a powerful machine in which a certain quantity of material must be furnished in order to produce the required amount of force. This important physiological fact is strikingly exemplified in armies; and the history of the world presents few examples of warlike operations in which the efficiency of the men has not been impaired by insufficient food.

The influence of diet upon the capacity for labor was well illustrated by a comparison of the amount of work accomplished by English and French laborers, in 1841, on a railway from Paris to Rouen. The French laborers engaged on this work were able at first to perform only about two-thirds of the labor accomplished by the English. It was suspected that this was due to the more substantial diet of the English, which proved to be the fact; for when the French laborers were subjected to a similar regimen, they were able to accomplish an equal amount of work. In all observations of this kind, it has been shown than an animal diet is much more favorable to the development of the physical forces than one consisting mainly of vegetables.

Climate has an important influence on the quantity of food demanded by the system. It is generally acknowledged that the consumption of all kinds of food is greater in cold than in warm climates, and almost every one has experienced in his own person a considerable difference in the appetite at different seasons of the year. Travelers' accounts of the quantity of food taken by the inhabitants of the frigid zone are almost incredible. They speak of men consuming more than a hundred pounds (45·36 kilos.) of meat in a day; and a Russian admiral, Saritcheff, gave an instance of a man who, in his presence, ate at a single meal a mess of boiled rice and butter weighing twenty-eight pounds (12·7 kilos.). Although it is difficult to regard these statements with entire confidence, the general opinion that the appetite is greater in cold than in warm climates is undoubtedly well founded. Hayes stated, from his personal observation, that the daily ration of the Esquimaux is twelve to fifteen pounds (5·443 to 6·804 kilos.), of meat, about one-third of which is fat. On one occasion he saw an Esquimau consume ten pounds (4·536 kilos.) of walrus-flesh and blubber at a single meal, which lasted, however, several hours. The continued low temperature he found had a remarkable effect on the tastes of his own party. With the thermometer ranging from $-60°$ to $-70°$ Fahr. ($-51°$ to $-57°$ C.), there was a persistent craving for a strong animal diet, particularly fatty substances. Some members of the party were in the habit of drinking the contents of the oil-kettle with evident relish.

*Necessity of a Varied Diet.*—In considering the nutritive value of the various alimentary substances, the fact that no single one of them is capable of supplying all the material for the regeneration of the organism has frequently been mentioned. The normal appetite, which is the best guide as regards the quantity and the selection of food, indicates that a varied diet is necessary to proper nutrition. This fact is exemplified in a marked degree in long voyages and in the alimentation of armies, when, from necessity or otherwise, the necessary variety of aliment is not presented. Analytical chemistry fails to show why this change in alimentation is necessary or in what the deficiency in a single kind of diet consists; but it is nevertheless true that after the organic constituents of the organism have appropriated the nutritious elements of particular kinds of food for a certain time, they lose the power of effecting the changes necessary to proper nutrition. This fact is particularly well marked when the diet consists in great part of salted meats, although it sometimes occurs when a single kind of fresh meat is constantly used. After long confinement to a diet restricted as regards variety, a supply of other matters, such as fresh vegetables, the organic acids, and articles which are called generally antiscorbutics, becomes indispensable; otherwise, the modifications in nutrition and in the constitution of the blood incident to the scorbutic condition are almost always developed.

It is thus apparent that adequate quantity and proper quality of food are not all that is required in alimentation; and those who have the responsibility of regulating the diet of a large number of persons must bear in mind the fact that the organism demands considerable variety. Fresh vegetables, fruits etc., should be taken at the proper seasons. It is almost always found, when there is of necessity some sameness of diet, that there is a craving for particular articles, and these, if possible, should be supplied. This was frequently exemplified in the civil war. At times when the diet was necessarily somewhat monotonous, there was an almost universal craving for onions and raw potatoes, which were found by army surgeons to be excellent antiscorbutics.

With those who supply their own food, the question of variety of diet generally regulates itself; and in institutions, it is a good rule to follow as far as possible the reasonable tastes of the inmates. In individuals, particularly females, it is not uncommon to observe marked disorders in nutrition attributable to want of variety in the diet as well as to an insufficient quantity of food as a matter of education or habit.

A full consideration of the varieties of food and of the different methods employed in its preparation belongs properly to special works on dietetics. Among the ordinary articles of diet, the most important are meats, bread, potatoes, milk, butter and eggs; and it is necessary only to treat of these very briefly.

*Meats.*—Among the various kinds of muscular tissue, beef has been found to possess the greatest nutritive value. Other varieties of flesh, even that of birds, fishes and animals in a wild state, do not present an appreciable difference, as far as can be ascertained by chemical analysis; but when taken daily for a long time, they become distasteful, the appetite fails, and the system seems to demand a change of diet. The flesh of carnivorous animals is rarely used as food; and animals that eat animal as well as vegetable food, such as pigs or ducks, acquire a disagreeable flavor when they are not fed on vegetables. Soups, broths, and most of the liquid extracts of meat really possess but little nutritive value and they can not replace the ordinary cooked meats. The following is the composition of roasted meat, no dripping being lost, according to the analysis of Ranke, quoted by Pavy:

| | |
|---|---|
| Nitrogenous matters | 27·60 |
| Fat | 15·45 |
| Saline matters | 2·95 |
| Water | 54·00 |
| | 100·00 |

*Bread.*—Bread presents a considerable variety of alimentary constituents and is a very important article of diet. The constituents of flour undergo peculiar changes in panification, which give to good bread its characteristic flavor. Bread, especially coarse, brown bread, as a single article of food, is capable of sustaining life for a long time. It contains a large proportion of starch, but its important nitrogenized constituent is gluten, which is not a simple substance but contains vegetable fibrin, vegetable albumen, a peculiar substance soluble in alcohol, called glutine, with fatty and inorganic matters. The following is the composition of bread, according to Letheby:

| | |
|---|---|
| Nitrogenized matters | 8·1 |
| Carbohydrates (chiefly starch) | 51·0 |
| Fatty matters | 1·6 |
| Saline matters | 2·3 |
| Water | 37·0 |
| | 100·0 |

*Potatoes.*—Potatoes are very useful as an article of diet, especially on account of the agreeable form in which starchy matter is presented; for they contain but a small proportion of nitrogenized matter and do not possess as much nutritive value as exists in bread. They are selected for description from the vegetable foods for the reason that they are almost universally used in civilized countries throughout the year. They are usually cooked thoroughly, but the raw potato is a valuable antiscorbutic. The following is the composition of potato, according to Letheby:

| | |
|---|---|
| Nitrogenized matter | 2·1 |
| Starchy matters | 18·8 |
| Sugar | 3·2 |
| Fat | 0·2 |
| Saline matters | 0·7 |
| Water | 75·0 |
| | 100·0 |

*Milk.*—Milk, and articles prepared from milk, such as butter, cheese etc., are important articles of food. In the treatment of disease, milk is frequently used as a single article of diet. On account of the great variety of alimentary matters which it contains, including a great number of inorganic salts and even a small quantity of iron, milk will meet all the nutritive demands of the system, probably for an indefinite time. It is largely used in the preparation of other articles of food by cooking. Pure butter, which represents the fatty constituents of milk, contains, in 100 parts, 30 parts of oleine, 68 parts of palmitine, and 2 parts of other fats peculiar to milk (Bromeis). The following is the composition of cow's milk, according to Letheby:

| | |
|---|---|
| Nitrogenized matters | 4·1 |
| Fatty matters | 3·9 |
| Sugar | 5·2 |
| Inorganic matters | 0·8 |
| Water | 86·0 |
| | 100·0 |

In connection with the composition of human milk, to be given farther on, the great variety of its constituents will be more fully considered.

*Eggs.*—As regards nutrition, the analogy between eggs and butter is evident when it is remembered that the constituents of eggs furnish materials for the growth of the chick, to which must be added certain saline matters absorbed from the shell during the process of incubation. Among the inorganic constituents of eggs, there is always a small quantity of iron. The following is the composition of the entire contents of the egg, quoted from Pavy:

| | |
|---|---|
| Nitrogenized matters | 14·0 |
| Fatty matters | 10·5 |
| Inorganic matters | 1·5 |
| Water | 74·0 |
| | 100·0 |

A number of different nitrogenized and fatty matters, a small quantity of saccharine matter, as well as a great variety of inorganic salts, exist in eggs.

The physiological effects of a diet restricted to a single constituent of food or to a few articles have been closely studied both in the human subject and in the inferior animals. Animals subjected to a diet composed exclusively of non-nitrogenized matters die in a short time with all the symptoms of inanition. The same result follows when dogs are confined to white bread and water; but these animals live very well on the military brown bread, as this contains a greater variety of alimentary matters (Magendie). Facts of this nature were multiplied by the "gelatine commission," and the experiments were extended to nitrogenized substances and articles containing a considerable variety of alimentary matters. In these experiments, it was shown that dogs could not live on a diet of pure myosine, the appetite entirely failing at the forty-third to the fifty-fifth day. They were nourished perfectly well by gluten, which is composed of a number of different alimentary substances. Among the conclusions arrived at by this commission, which bear particularly on the questions under consideration, were the following:

"Gelatine, albumen, fibrin, taken separately, do not nourish animals except for a very limited period and in a very incomplete manner. In general, these substances soon excite an insurmountable disgust, to the point that animals prefer to die of hunger rather than touch them.

"The same substances artificially combined and rendered agreeably sapid by seasoning are accepted more readily and longer than if they were isolated, but ultimately they have no better influence on nutrition, for animals that take them, even in considerable quantity, finally die with all the signs of complete inanition.

"Muscular flesh, in which gelatine, albumen and fibrin are united according to the laws of organic nature, and when they are associated with other matters, such as fat, salts etc., suffices, even in very small quantity, for complete and prolonged nutrition."

In Burdach's treatise on physiology, is an account of some interesting experiments by Ernest Burdach on rabbits, showing the influence of a restricted diet upon nutrition. Three young rabbits from the same litter were experimented upon. One was fed with potato alone and died on the thirteenth day, with all the appearances of inanition. Another fed on barley alone died in the same way during the fourth week. The third was fed alternately day by day with potato and barley, for three weeks, and afterward with potato and barley given together. This animal increased in size and was perfectly well nourished.

In 1769, long before any of the above-mentioned experiments were performed, Dr. Stark, a young English physiologist, fell a victim at an early age to experiments on his own person on the physiological effects of different kinds of food. He lived for forty-four days on bread and water, for twenty-nine days on bread, sugar and water, and for twenty-four days on bread, water and olive-oil; until finally his constitution became broken, and he died from the effects of his experiments.

## CHAPTER VII.

### *DIGESTION—MASTICATION, INSALIVATION AND DEGLUTITION.*

Prehension of food—Mastication—Physiological anatomy of the teeth—Anatomy of the maxillary bones—Temporo-maxillary articulation—Muscles of mastication—Action of the tongue, lips and cheeks in mastication—Parotid saliva—Submaxillary saliva—Sublingual saliva—Fluids from the smaller glands of the mouth, tongue and fauces—Mixed saliva—Quantity of saliva—General properties and composition of the saliva—Action of the saliva on starch—Uses of the saliva—Physiological anatomy of the parts concerned in deglutition—Mechanism of deglutition—First period of deglutition—Second period of deglutition—Protection of the posterior nares during the second period of deglutition—Protection of the opening of the larynx and uses of the epiglottis in deglutition—Third period of deglutition—Deglutition of air.

INORGANIC alimentary substances are, with few exceptions, introduced in the form in which they exist in the blood and require no preparation or change before they are absorbed; but organic nitrogenized substances are always united with more or less matter possessing no nutritive properties, from which they must be separated, and even when pure, they always undergo certain changes before they are taken up by the blood. The non-nitrogenized matters also undergo changes in constitution or in form preparatory to absorption.

*Prehension of Food.*—Prehension of food in the adult is a process so simple and well known that it demands little more than a passing mention. The mechanism of sucking in the infant and of drinking is a little more complicated. In sucking, the lips are closed around the nipple, the velum pendulum palati is applied to the back of the tongue so as to close the buccal cavity posteriorly, and the tongue, acting as a piston, produces a virtual vacuum in the mouth, by which the liquids are drawn in with considerable force. This may be done independently of the act of respiration, which is necessarily arrested only during deglutition; for the mere act of suction has never anything to do with the condition of the thoracic walls. The mechanism of drinking from a vessel is essentially the same. The vessel is inclined so that the lips are kept covered with the liquid and are closed around the edge. By a gentle, sucking action the liquid is then introduced. This is the ordinary mechanism of drinking; but sometimes the head is thrown back and the liquid is poured into the mouth, as in "tossing off" the contents of a small vessel.

## MASTICATION.

In order that digestion may take place in a perfectly natural manner, it is necessary that the food, as it is received into the stomach, should be so far comminuted and incorporated with the fluids of the mouth as to be readily acted upon by the gastric juice; otherwise, gastric digestion is prolonged and difficult. Non-observance of this physiological law is a frequent cause of what is generally called dyspepsia.

*Physiological Anatomy of the Organs of Mastication.*—In the adult, each jaw is provided with sixteen teeth, all of which are about equally developed. The canines, so largely developed in the carnivora but which are rudimentary in the herbivora, and the incisors and molars, so fully developed in the herbivora, are, in man, of nearly the same length. Each tooth presents for anatomical description a crown, a neck and a root, or fang. The crown is that portion which is entirely uncovered by the gums; the root is that portion embedded in the alveolar cavities of the maxillary bones; and the neck is the portion, sometimes slightly constricted, situated between the crown and the root and covered by the edge of the gum. Each tooth presents, on section, several distinct structures.

*Enamel of the Teeth.*—The crown is covered by the enamel, which is by far the hardest structure in the economy. This is white and glistening and is thickest on the lower portion of the tooth, especially over the surfaces which, from being opposed to each other on either jaw, are most exposed to wear. It here exists in several concentric layers. The incrustation of enamel becomes gradually thinner toward the neck, where it ceases. The enamel is made up of pentagonal or hexagonal rods, one end resting upon the subjacent structure, and the other, when there exists but a single layer of enamel, terminating just beneath the cuticle of the teeth.

The exposed surfaces of the teeth are still farther protected by a membrane, $\frac{1}{30000}$ to $\frac{1}{15000}$ of an inch (0·8 to 1·7 $\mu$) in thickness, closely adherent to the enamel, called the cuticle of the enamel (Nasmyth's membrane). The cuticle presents a strong resistance to reagents and is useful in protecting the teeth from the action of acids which may find their way into the mouth.

*Dentine.*—The largest portion of the teeth is composed of dentine, or ivory. In many respects, particularly in its composition, this resembles bone; but it is much harder and does not possess the lacunæ and canaliculi which are characteristic of the true osseous structure. The dentine bounds and encloses the central cavity of the tooth, extending in the crown to the enamel, and in the root, to the cement. It is formed of a homogeneous, fundamental substance, which is penetrated by a large number of canals radiating from the pulp-cavity toward the exterior. These are called the dentinal tubules or canals. They are $\frac{1}{25000}$ to $\frac{1}{12000}$ of an inch (1 to 2 $\mu$) in diameter, with walls of a thickness a little less than their caliber. Their course is slightly wavy or spiral. Beginning at the pulp-cavity, into which these canals open, they are found to branch and occasionally anastomose, their communications and branches becoming more frequent as they approach the external surface of the tooth. The canals of largest diameter are found next the pulp-cavity, and they become smaller as they branch. The structure which forms the walls of these tubules is somewhat denser than the intermediate portion, which is sometimes called the intertubular substance of the dentine; but in some portions of the tooth, the tubules are so abundant that their walls touch each other, and there is, therefore, no intertubular substance. Near the origin and near the peripheral terminations of the dentinal tubules, are sometimes found solid, globular masses of dentine, called dentine-globules, which irregularly bound triangular or stellate cavities of very variable size. Sometimes these cavities form regular zones near the peripheral termination of the tubules. The dentine is sometimes marked by concentric lines, indicating a lamellated arrangement. In the natural condition, the dentinal tubules are filled with a clear liquid, which penetrates from the vascular structures in the pulp-cavity.

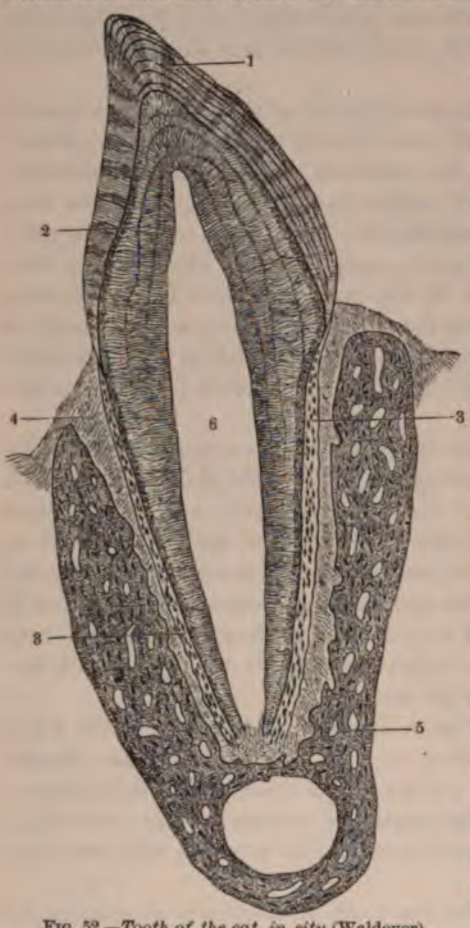

FIG. 52.—*Tooth of the cat, in situ* (Waldeyer).
1, enamel; 2, dentine; 3, cement; 4, periosteum of the alveolar cavity; 5, lower jaw; 6, pulp-cavity.

*Cement.*—Covering the dentine of the root, is a thin layer of true bony structure, called the cement, or crusta petrosa. This is thickest at the summit and at the deeper portions of the root, where it is sometimes lamellated, and it becomes thinner near the neck. It finally becomes continuous with the enamel of the crown, so that the dentine is everywhere completely covered. The cement is closely adherent to the dentine and to the periosteum lining the alveolar cavities.

*Pulp-Cavity.*—In the interior of each tooth, extending from the apex of the root or roots into the crown, is the pulp-cavity, which contains minute blood-vessels and nervous filaments, held together by longitudinal fibres of connective tissue. This is the only portion of the tooth endowed with sensibility. The blood-vessels and nerves penetrate by a little orifice at the extremity of each root.

The dentine and enamel of the teeth must be regarded as perfected structures; for when the second, or permanent teeth are lost, they are never reproduced, and when these parts are invaded by wear or by decay, they are not restored.

The thirty-two permanent teeth are classified as follows:

1. Eight incisors, four in each jaw, called the central and lateral incisors.

2. Four canines, or cuspidati, two in each jaw, just back of the incisors. The upper canines are sometimes called the eye-teeth, and the lower canines, the stomach-teeth.

3. Eight bicuspid—the small, or false molars—just back of the canines; four in each jaw.

4. Twelve molars, or multicuspid, situated just back of the bicuspid; six in each jaw.

The incisors are wedge-shaped, flattened antero-posteriorly, and bevelled at the expense of the posterior face, giving them a sharp, cutting edge, which is sometimes perfectly straight but is generally more or less rounded. Each incisor has a single root. The special use of the incisor teeth is to divide the food as it is taken into the mouth. The permanent incisors make their appearance between the seventh and the eighth years.

The canines are more conical and pointed than the incisors, and have longer and larger roots, especially those in the upper jaw. Their roots are single. They are used, with the incisors, in dividing the food. The permanent canines make their appearance between the eleventh and the twelfth years.

The bicuspid teeth are shorter and thicker than the canines. Their opposed surfaces are rather broad and are marked by two eminences. The upper bicuspids are larger than the lower. The roots are single, but in the upper jaw they are slightly bifurcated at their extremities. They are used, with the true molars, in triturating the food. The permanent bicuspids make their appearance between the ninth and the tenth years.

The molar teeth, called respectively—counting from before backward—the first, second and third molars, are the largest of all and are, *par excellence*, the teeth used in mastication. Their form is that of a cube, rounded laterally and provided with four or five eminences on their opposed surfaces. The first molars are the largest. They have generally three roots in the upper jaw and two in the lower, although they sometimes have four or even five roots. The second molars are but little smaller than the first and resemble them in nearly every particular. The third molars, called frequently the wisdom-teeth, are much smaller than the others and are by no means so useful in mastication. The first molars are the first of the permanent teeth, making their appearance between the sixth and the seventh years. The second molars appear between the twelfth and the thirteenth years; and the third molars, between the seventeenth and the twenty-first years, and sometimes even much later. In some instances the third molars are never developed.

The upper jaw has ordinarily a somewhat longer and broader arch than the lower; so that when the mouth is closed the teeth are not brought into exact apposition, but the upper teeth overlap the lower teeth both in front and laterally. The lower teeth are all somewhat smaller than the corresponding teeth in the upper jaw and generally make their appearance a little earlier.

The physiological anatomy of the maxillary bones and of the temporo-maxillary articulation necessarily precedes the study of the muscles of mastication and the mechanism of their action.

The superior maxillary bones are immovably articulated with the other bones of the head, and do not usually take any active part in mastication. Their inferior borders, with the upper teeth embedded in the alveolar cavities, present fixed surfaces against which the food is pressed by the action of the muscles which move the lower jaw.

The inferior maxilla is a single bone. Its body is horizontal, of a horse-shoe shape, and in the alveolar cavities in its superior border, are the lower teeth. Below the teeth, both externally and internally, are surfaces for the atachments of the muscles concerned in the various movements of the jaw and for one of the muscles of the tongue.

FIG. 53.—*Inferior maxilla* (Sappey).
1, body; 2, ramus; 3, symphysis; 4, incisive fossa; 5, mental foramen; 6, attachment of the digastric muscle; 7, depression at the site of the facial artery; 8, angle; 9, attachment of the superior constrictor of the pharynx; 10, coronoid process; 11, condyle; 12, sigmoid notch; 13, opening of the inferior dental canal; 14, groove for the mylo-hyoid muscle; 15, alveolar border; i, incisor teeth; c, canine teeth; b, bicuspid teeth; m, molars.

*Temporo-Maxillary Articulation.*—In man the articulation of the lower jaw with the temporal bone is such as to allow an antero-posterior sliding movement and a lateral movement, in addition to the movements of elevation and depression. The condyloid process is convex, with an ovoid surface, the general direction of its long diameter being transverse, and slightly oblique from without inward and from before backward. This process is received into a cavity of corresponding shape in the temporal bone, the glenoid fossa, which is bounded anteriorly by a rounded eminence, called the eminentia articularis.

Between the condyle of the lower jaw and the glenoid fossa, is an oblong, interarticular disk of fibro-cartilage. This disk is thicker at the edges than in the centre. It is pliable and is so situated that when the lower jaw is projected forward, making the lower teeth project beyond the upper, it is applied to the convex surface of the eminentia articularis and presents a concave surface for articulation with the condyle. One of the uses of this cartilage is to constantly present a proper articulating surface upon the articular eminence and thus permit the antero-posterior sliding movement of the lower jaw. It is also important in the lateral movements of the jaw, in which one of the condyles remains in the glenoid cavity and the other is projected, so that the bone undergoes a slight rotation.

*Muscles of Mastication.*—To the lower jaw are attached certain muscles by which it is depressed, and others by which it is elevated, projected forward, drawn backward and moved from side to side. The following are the principal muscles concerned in the production of these varied movements:

MUSCLES OF MASTICATION.

*Muscles which depress the lower jaw.*

| MUSCLE. | ATTACHMENTS. |
|---|---|
| Digastric | Mastoid process of the temporal bone—Lower border of the inferior maxilla near the symphysis, with its central tendon held to the side of the body of the hyoid bone. |
| Mylo-hyoid | Body of the hyoid bone—Mylo-hyoid ridge on the internal surface of the inferior maxilla. |
| Genio-hyoid | Body of the hyoid bone—Inferior genial tubercle on the inner surface of the inferior maxilla, near the symphysis. |
| Platysma myoides | Clavicle, acromion and fascia—Anterior half of the body of the inferior maxilla, near the inferior border. |

*Muscles which elevate the lower jaw and move it laterally and antero-posteriorly.*

| | |
|---|---|
| Temporal | Temporal fossa—Coronoid process of the inferior maxilla. |
| Masseter | Malar process of the superior maxilla, lower border and internal surface of the zygomatic arch—Surface of the ramus of the inferior maxilla. |
| Internal pterygoid | Pterygoid fossa—Inner side of the ramus, and angle of the inferior maxilla. |
| External pterygoid | Pterygoid ridge of the sphenoid, the surface between it and the pterygoid process, external pterygoid plate, tuberosity of the palate and the superior maxillary bone—Inner surface of the neck of the condyle of the inferior maxilla and the interarticular fibro-cartilage. |

*Action of the Muscles which depress the Lower Jaw.*—The most important of these muscles have for their fixed point of action, the hyoid bone, which is fixed by the muscles extending from it to the upper part of the chest. The central tendon of the digastric, as it perforates the stylo-hyoid, is connected with the hyoid bone by a loop of fibrous tissue; and acting from this bone as the fixed point, the anterior belly must of necessity tend to depress the jaw. The attachments of the mylo-hyoid and the genio-hyoid render their action in depressing the jaw sufficiently evident, which is also the case with the platysma myoides, acting from its attachments to the upper part of the thorax. In ordinary mastication the upper jaw undergoes a slight movement of elevation, and this becomes somewhat exaggerated when the mouth is opened to the fullest possible extent.

*Action of the Muscles which elevate the Lower Jaw and move it laterally and antero-posteriorly.*—The temporal, masseter and internal pterygoid muscles are chiefly concerned in the simple act of closing the jaws. Their anatomy alone gives a sufficiently clear idea of their mode of action; and their great power is explained by the number of their fibres, by the attachments of many of these fibres to the strong aponeuroses by which they are covered, and by the fact that the distance from their origin to their insertion is very short.

The attachments of the internal and external pterygoids are such that by their alternate action on either side, the jaw may be moved laterally, as their points of origin are situated in front of and internal to the temporo-maxillary articulation. The articulation of the lower jaw is of such a kind that in its lateral movements the condyles themselves can not be sufficiently displaced from side to side; but with the condyle on one side fixed or moved slightly backward, the other may be brought forward against the articular eminence, producing a movement of rotation.

The above explanation of the lateral movements of the jaw presupposes the possibility of movements in an antero-posterior direction. Movements in a forward direction, so as to make the lower teeth project beyond the upper, are effected by the pterygoids, the oblique fibres of the masseter and the anterior fibres of the temporal. By the combined action of the posterior fibres of the temporal, the digastric, mylo-hyoid and genio-hyoid, the jaw is brought back to its position. By the same action it may also be drawn back slightly from its normal position while at rest.

*Action of the Tongue, Lips and Cheeks, in Mastication.*—Experiments on living animals and phenomena observed in cases of lesions of the nervous system in the human subject have shown the importance of the tongue and cheeks in mastication. Section of the facial nerves is a common physiological experiment. Operations of this kind, and cases of facial palsy, which are not uncommon in the human subject, show that when the cheek is paralyzed the food accumulates between it and the teeth, producing great inconvenience.

The varied and complex movements of the tongue during mastication are not easily described. After solid food is taken into the mouth, the tongue prevents its escape from between the teeth, and by its constant movements, rolls the alimentary bolus over and over and passes it at times from one side to the other, so that the food may undergo thorough trituration. Aside from the uses of the tongue as an organ of taste, its surface is endowed with peculiar sensibility as regards the consistence, size and form of different articles; and this is undoubtedly important in determining when mastication is completed, although the thoroughness with which mastication is accomplished is much influenced by habit.

Tonic contraction of the orbicularis oris is necessary to keep the fluids within the mouth during repose; and this muscle is sometimes brought into action when the mouth is very full, to assist in keeping the food between the teeth. This latter office, however, is performed mainly by the buccinator; the action of which is to press the food between the teeth and keep it in place during mastication, assisting, from time to time, in turning the alimentary bolus so as to subject new portions to trituration.

The process of mastication is regulated to a very great extent by the sensibility of the teeth to the impressions of hard and soft substances. It is only necessary to call attention to the ease and certainty with which the presence and the consistence of the smallest substance between the teeth are recognized, to show the importance of this tactile sense in mastication.

## Saliva.

The fluid which is mixed with the food in mastication, which moistens the mucous membrane of the mouth and which may be collected at any time in small quantity by the simple act of sputation, is composed of the secretions of a considerable number and variety of glands. The most important of these are the parotid, submaxillary and sublingual, which are usually called the salivary glands. The labial and buccal glands, the glands of the tongue and general mucous surface and certain glandular structures in the mucous membrane of the pharynx also contribute to the production of the saliva. The liquid which becomes more or less incorporated with the food before it descends to the stomach, and which must be regarded as the digestive fluid of the mouth, is known as the mixed saliva; but the study of the composition and properties of this fluid as a whole should be prefaced by a consideration of the different secretions of which it is composed. The salivary glands belong to the variety of glands called racemose. They resemble the other glands belonging to this class, and their structure will be more fully considered in connection with the physiology of secretion.

Fig. 54.—*Salivary glands* (Tracy).

*Parotid Saliva.*—The parotid is the largest of the three salivary glands. It is situated below and in front of the ear and opens by the duct of Steno into the mouth, at about the middle of the cheek. The papilla which marks the orifice of the duct is situated opposite the second large molar tooth of the upper jaw.

The organic matter of the parotid saliva is coagulable by heat (212° Fahr., or 100° C.), alcohol or the strong mineral acids. A compound of sulphocyanogen is now generally acknowledged to be a constant constituent of the parotid saliva. This can not be recognized by the ordinary tests in the fresh saliva taken from the duct of Steno, but in the clear, filtered fluid which passes after the precipitation of the organic matter, there is always a distinct, red color on the addition of ferric sulphate. As this reaction is more marked in the mixed saliva, the methods by which the presence of a sulphocyanide is to be recognized will be considered in connection with that fluid. In the human subject, the parotid secretion is more abundant than that of any other of the salivary glands; but the entire quantity in the twenty-four hours has not been directly estimated.

In the horse, ass and ox, it has been found that when mastication is performed on one side of the mouth, the flow from the gland on that side is greatly increased, exceeding by several times the quantity produced upon the opposite side (Colin). This fact has been confirmed by Dalton in the human subject.

The flow of saliva from the parotid takes place with greatly increased activity during the process of mastication. The orifice of the parotid duct is so situated that the fluid is poured directly upon the mass of food as it is undergoing trituration by the teeth; and as the secretion is more abundant on the side on which mastication is going on, and the consistence of the fluid is such as to enable it to mix readily with the food, the office of this gland is supposed to be particularly connected with mastication. This is undoubtedly the fact; although its flow is not absolutely confined to the period of mastication, but continues in small quantity during the intervals. Its quantity is regulatėd somewhat by the character of the food, being much greater when the articles taken into the mouth are dry than when they contain considerable moisture. In the human subject, the stimulus produced by sapid substances will sometimes cause a great increase in the flow of the parotid saliva. Mitscherlich and Eberle observed this in persons suffering from salivary fistula and noted, farthermore, that the mere sight or odor of food produced the same effect. The supposition that the flow from the parotid is dependent upon the mechanical pressure of the muscles or of the condyle of the lower jaw during mastication has no foundation in fact. In the horse and in the dog, it has been observed that the secretion of the parotids is completely arrested during the deglutition of liquids, while the flow from the other salivary glands is not affected (Bernard).

The parotid saliva—aside from any chemical action which it may have upon the food, which will be fully considered in connection with the mixed saliva—evidently has an important mechanical office. It is discharged in large quantity during the act of mastication and is poured into the mouth in such a manner as to become of necessity thoroughly incorporated with the food. Its use is chiefly, although not exclusively, connected with mastication and indirectly, with deglutition; for it is only by becoming incorporated with this saliva, that dry, pulverulent substances can be swallowed.

*Submaxillary Saliva.*—In the human subject, the submaxiliary is the second of the salivary glands in point of size. Its minute structure is nearly the same as that of the parotid. As its name implies, it is situated below the inferior maxillary bone. It is in the anterior part of what is known as the submaxillary triangle of the neck. Its excretory duct, the duct of Wharton, is about two inches (5 centimetres) in length and passes from the gland, beneath the tongue, to open by a small papilla by the side of the frenum.

The pure submaxillary saliva presents many important points of difference from the secretion of the parotid. It may be obtained by exposing the duct and introducing a fine silver tube, when, on the introduction of any sapid substance into the mouth, the secretion will flow in large, pearly drops. This variety of saliva is much more viscid than the parotid secretion. It is perfectly clear, and on cooling, it frequently becomes of a gelatinous consistence. Its organic matter is not coagulable by heat. It contains a sulphocyanide, but in very small quantity.

The submaxillary gland pours out its secretion in greatest abundance when sapid substances are introduced into the mouth; but unlike the parotid saliva, the secretion does not alternate on the two sides with alternation in mastication. Although sapid articles excite an abundant secretion from the submaxillary glands, they also increase the secretions from the parotids and sublinguals; and on the other hand, movements of mastication increase somewhat the flow from the submaxillaries, and these glands secrete a certain quantity of fluid during the intervals of digestion. The viscid consistence of the submaxillary saliva renders it less capable than the parotid secretion of penetrating the alimentary mass during mastication.

*Sublingual Saliva.*—The sublinguals, the smallest of the salivary glands, are situated beneath the tongue, on either side of the frenum. In minute structure they resemble the parotid and the submaxillary glands. Each gland has a number of excretory ducts, eight to twenty, which open into the mouth by the side of the frenum; and one of the ducts, larger than the others, joins the duct of the submaxillary gland near its opening in the mouth.

The secretion of the sublingual glands is more viscid, even, than the submaxillary saliva, but it differs in the fact that it does not gelantinize on cooling. It is so glutinous that it adheres strongly to any vessel and flows with difficulty from a tube introduced into the duct. Like the secretion from the other salivary glands, its reaction is distinctly alkaline. Its organic matter is not coagulable by heat, acids or the metallic salts.

It has been shown that the sublingual glands may be excited to secretion by impressions made by sapid substances upon the nerves of taste, although the flow is always less than from the submaxillary glands. The great viscidity of the sublingual saliva renders it less easily mixed with the alimentary bolus than the secretions from the parotid or the submaxillary glands.

*Fluids from the Smaller Glands of the Mouth, Tongue and Pharynx.*—Beneath the mucous membrane of the inner surface of the lips, are small, rounded, glandular bodies, opening into the buccal cavity, called the labial glands; and in the submucous tissue of the cheeks, are similar bodies, called the buccal glands. The latter are somewhat smaller than the labial glands. Two or three of the buccal glands are of considerable size and have ducts opening opposite the last molar tooth. These are sometimes distinguished as the molar glands. There are also a few small glands in the mucous membrane of the posterior half of the hard palate; but the glands on the under surface of the soft palate are larger and here form a continuous layer. The glands of the tongue are situated beneath the mucous membrane, mainly on the posterior third of the dorsum; but a few are found at the edges and the tip, and there is a gland of considerable size on either side of the frenum, near the tip. All of these are small, racemose glands, similar in structure to those which have been called the true salivary glands. In addition to these structures, the mucous membrane of the tongue is provided with simple and compound follicular glands, which extend over its entire surface, but are most abundant at the posterior portion, behind the circumvallate papillæ. The most important of the glands of the tongue will be described in connection with the physiology of gustation.

In the pharynx and the posterior portion of the buccal cavity, are the pharyngeal glands and the tonsils. In the pharynx, particularly the upper portion, racemose glands, like those found in the mouth, exist in large numbers. The mucous membrane is provided, also, with simple and compound mucous follicles. The tonsils, situated on either side of the fauces between the pillars of the soft palate, consist of an aggregation of compound follicular glands. The number of glands entering into the composition of each tonsil is ten to twenty.

The secretion from the glands and follicles above enumerated can not be obtained, in the human subject, unmixed with the fluids from the true salivary glands. It has been collected in small quantity, however, from the inferior animals, after ligature of all the salivary ducts. This secretion is simply a grayish, viscid mucus, containing a number of leucocytes and desquamated epithelial scales. It is this which gives the turbid and opaline character to the mixed saliva, as the secretions of the salivary glands are all perfectly transparent. The fluid from these glands in the mouth is mixed with the salivary secretions; and that from the posterior part of the tongue, the tonsils, and the pharyngeal glands passes down to the stomach with the alimentary bolus. This secretion, consequently, forms a constant and essential part of the mixed saliva.

*Mixed Saliva.*—Although the study of the distinct secretions discharged into the mouth possesses considerable physiological importance, it is only the fluid resulting from a union of them all, which can properly be considered in connection with the general process of insalivation. In man it is necessary that the cavity of the mouth should be continually moistened, if for nothing else, to keep the parts in a proper condition for phonation. A little reflection will make it apparent that the flow, from some of the glands at least, is constant, and that from time to time a certain quantity of saliva is swallowed. The discharge of the fluid into the mouth, though diminished, is not arrested during sleep. In the review of the different kinds of saliva, it has been seen that the flow from none of the glands is absolutely intermittent; unless it be so occasionally from the parotid, the secreting action of which is most powerfully influenced by the act of mastication and the impression of sapid substances.

Upon the introduction of food the quantity of saliva is greatly increased; and the influence of the sight, odor, and occasionally even the thought of agreeable articles has already been mentioned. The experiments of Frerichs on dogs with gastric fistulæ, and the observations of Gardner on a patient with a wound in the œsophagus, have demonstrated that the flow of saliva may be excited by the stimulus of food introduced directly into the stomach without passing through the mouth.

*Quantity of Saliva.*—It is not easy to estimate in the human subject the entire quantity of saliva secreted in the twenty-four hours; and great variations in this regard undoubtedly exist in different persons and even in the same individual at different times. An approximate estimate may be arrived at by noting as nearly as possible the average quantity secreted during the intervals of digestion and adding to it the quantity absorbed by the various articles of food. Estimates of this kind can be approximate only, and those made by Dalton are apparently the most satisfactory. The following represents, according to Dalton, the quantities of saliva secreted during mastication and during the intervals of meals:

| | | |
|---|---|---|
| Saliva required for mastication...................... | 17·32 oz. | (491 grammes). |
| Saliva secreted in intervals of meals................ | 27·93 oz. | (792 grammes). |
| Total quantity per day........................ | 45·25 oz. | (1,283 grammes). |

The total daily quantity of saliva, therefore, is a little more than two and three-fourths pounds.

Remembering that the quantity of saliva must necessarily be subject to great variations, this estimate may be taken as giving a sufficiently close approximation of the quantity of saliva ordinarily secreted. It must be borne in mind, however, with reference to this and the other digestive secretions, that this large quantity of fluid is at no one time removed from the blood but is reabsorbed nearly as fast as secreted, and that normally, none of it is discharged from the organism.

*General Properties and Composition of the Saliva.*—The mixed fluid taken from the mouth is colorless, somewhat opaline, frothy and slightly viscid. It generally has a faint and somewhat disagreeable odor very soon after it is discharged. If it be allowed to stand, it deposits a whitish sediment, composed mainly of desquamated epithelial scales with a few leucocytes, leaving the supernatant fluid tolerably clear. Its specific gravity is variable, ranging between 1004 or 1006 and 1008. Its reaction is almost constantly alkaline; although, under certain abnormal conditions of the system, it has occasionally been observed to be neutral, and sometimes, though rarely, acid. The saliva becomes slightly opalescent by boiling or on the addition of strong acids. The addition of absolute alcohol produces an abundant, whitish, flocculent precipitate. Almost invariably the mixed saliva presents a more or less intense blood-red tint on the addition of a per-salt of iron, which is due to the presence of a sulphocyanide either of potassium or of sodium.

A number of analyses of the human mixed saliva have been made by different chemists, presenting, however, few differences, except in the relative proportions of water and solid ingredients, which are probably quite variable. The following is an analysis by Bidder and Schmidt:

COMPOSITION OF HUMAN SALIVA.

| | |
|---|---|
| Water | 995·16 |
| Epithelium | 1·62 |
| Soluble organic matter | 1·34 |
| Potassium sulphocyanide | 0·06 |
| Sodium, calcium and magnesium phosphates | 0·98 |
| Potassium chloride / Sodium chloride | 0·84 |
| | 1,000·00 |

The organic matter of the mixed saliva, called by Berzelius, ptyaline, on the addition of an excess of absolute alcohol, is coagulated in the form of whitish flakes which may be readily separated by filtration. This substance has been studied by Mialhe and is described by him under the name of animal diastase. This author regards it as the active principle of the saliva. It has no direct influence upon the nitrogenized alimentary matters, but when brought in contact with hydrated starch, readily transforms it, first into dextrine and afterward into glucose. According to Mialhe, the energy of this action is such that one part is sufficient to effect the transformation of more than two thousand parts of starch.

The presence of a certain quantity of potassium sulphocyanide in the mixed saliva can be demonstrated by the addition of a per-salt of iron. That this is a constant and normal ingredient of the human saliva, can not be doubted.

Very little need be said concerning the other inorganic constituents of saliva, except that they are of such a nature as almost invariably to render the fluid distinctly alkaline. They exist in small proportion and do not appear to be connected in any way with the action of the saliva as a digestive fluid.

## Uses of the Saliva.

In 1831, Leuchs discovered that hydrated starch, mixed with fresh saliva and warmed, became liquid and was converted into sugar. This fact has since been repeatedly confirmed; and it is now a matter of common observation that hydrated starch or unleavened bread, taken into the mouth, almost instantly loses the property of striking a blue color with iodine and responds to the ordinary tests for sugar. Of the rapidity of this action any one can easily convince himself by the simple experiment of taking a little cooked starch into the mouth, mixing it well with the saliva, and testing in the ordinary way for sugar. This can hardly be done so rapidly that the reaction is not manifested, and the presence of sugar is also indicated by the taste. Although the human mixed saliva will finally exert the same action on uncooked starch, the transformation takes place much more slowly.

It has been shown that all the varieties of human saliva have the same effect on starch as the mixed fluids of the mouth. Dalton found no difference between the pure parotid saliva and the mixed saliva of the human subject, as regards the power of transforming starch into sugar. Bernard obtained the pure secretions from the parotid and from the submaxillary glands in the human subject, by drawing the fluids out of the ducts as they open into the mouth, by means of a small syringe with the nozzle arranged so as to fit over the papillæ, and demonstrated their action on starch. Longet showed that a mixture of the secretions of the submaxillary and the sublingual glands has the same property.

Several carbohydrates are formed as intermediate products between the hydrated starch and glucose, which latter is the final result of the action of the salivary ferment. After passing through one or two conditions slightly different from that of pure dextrine, the starch is converted into dextrine, which is changed into maltose ($C_{12}H_{22}O_{11}$), and the maltose is finally converted into glucose ($C_6H_{12}O_6$). This action is due entirely to the presence of ptyaline, although its intensity is increased in moderately alkaline solutions or by the addition of certain salts, especially sodium chloride. Feeble acids diminish the activity of this change, and it is arrested by strong mineral acids; although direct experiments have shown that the action of the saliva is slowly and feebly continued in the stomach. The temperature at which the action of the salivary ferment is most vigorous is about 100° Fahr. (38° C.); and any considerable variation from this temperature arrests the process.

In early infancy the action of the saliva upon starch is not so vigorous as in the adult, and it is said that immediately after birth the parotid secretion is the only one of the salivary fluids which contains ptyaline. In a few months, however, ptyaline appears in the submaxillary and sublingual secretions.

It is evident that the saliva, in addition to its mechanical action, transforms a considerable portion of the cooked starch, which is the common form in which starch is taken by the human subject, into sugar; but it is by no means the only fluid engaged in its digestion, similar properties belonging to the pancreatic and the intestinal juices. The last-named fluids are probably more active, even, than the saliva. The saliva acts slowly and imperfectly on raw starch, which becomes hydrated in the stomach and is digested mainly by the fluids of the small intestine. In all probability the saliva does not digest all the hydrated starch taken as food, the greater part passing unchanged from the stomach into the intestine. Those who attribute merely a mechanical action to the saliva draw their conclusions entirely from experiments on the lower animals, particularly the carnivora; and such observations can not properly be applied to the human subject.

In treating of the various fluids which are combined to form the mixed saliva, their mechanical uses have necessarily been touched upon. To sum up this part of the subject, however, it may be stated that the fluids of the mouth and pharynx have quite as important an office in preparing the food for deglutition and for the action of the juices in the stomach as in the digestion of starch. It is a matter of common experience that the rapid deglutition of very dry articles is impossible. In the human subject, although mastication and insalivation are by no means so complete as in some of the lower animals, the quantity of saliva absorbed by the various articles of food is very large. It seems impossible that the fluid thus incorporated with the food should not have an important influence on the changes which take place in the stomach, although it must be confessed that information on this point is very meagre, except as regards the digestion of starch.

It is undoubtedly the abundant secretion of the parotid glands which becomes most completely incorporated with the food during mastication and which serves to unite the dry particles into a coherent mass. The secretions from the submaxillary and sublingual glands and from the small glands and follicles of the mouth, being more viscid and less in quantity than the parotid secretion, penetrate the alimentary bolus less easily and form a glairy coating on its exterior, agglutinating the particles near the surface with peculiar tenacity.

When the processes of mastication and insalivation have been completed, and the food has passed into the pharynx, it meets with the secretion of the pharyngeal glands, which still farther coats the surface with the viscid fluid which covers the mucous membrane in this situation, thus facilitating the first processes of deglutition.

It has been observed that the saliva engages bubbles of air in the alimentary mass. In mastication, a considerable quantity of air is mixed with the food, and this facilitates the penetration of the gastric juice. It is well known that moist, heavy bread, and articles that can not become impregnated in this way with air, are not easily acted upon in the stomach.

## Deglutition.

Deglutition is the act by which solid and liquid articles are passed from the mouth into the stomach. The process involves first, the passage, by an automatic movement, of the alimentary mass through the isthmus of the fauces into the pharynx; then a rapid contraction of the constrictors of the pharynx, by which it is forced into the œsophagus; and finally, a peristaltic action of the muscular walls of the œsophagus, extending from its opening at the pharynx to the stomach.

*Physiological Anatomy of the Parts concerned in Deglutition.*—The parts concerned in this process are the tongue, the muscular walls of the pharynx and the œsophagus. In the passage of food and drink through the pharynx, it is necessary to completely protect from the entrance of foreign matters a number of openings which are exclusively for the passage of air. These are the posterior nares and the Eustachian tubes above, and the opening of the larynx below.

The tongue—a muscular organ capable of a great variety of movements—is the chief agent in the first processes of deglutition. A study of the muscles which are brought into action in deglutition would involve an anatomical description so elaborate as to be out of place in this work. The movements of the tongue, however, will be described in connection with the mechanism of deglutition.

The pharynx, in which the most complex of the movements of deglutition take place, is an irregular, funnel-shaped cavity, its longest diameter being transverse and opposite the cornua of the hyoid bone, with its smallest portion at the opening into the œsophagus. Its length is about four and a half inches (11·43 centimetres). It is connected superiorly and posteriorly with the basilar process of the occipital bone and with the upper cervical vertebræ. It is incompletely separated from the cavity of the mouth by the velum pendulum palati, a movable, musculo-membranous fold continuous with the roof of the mouth and marked by a line in the centre, which indicates its original development by two lateral halves. This, which is called the soft palate, when relaxed, presents a concave surface looking toward the mouth, a free, arched border, and a conical process hanging from the centre, called the uvula. On either side of the soft palate, are two curved pillars, or arches.

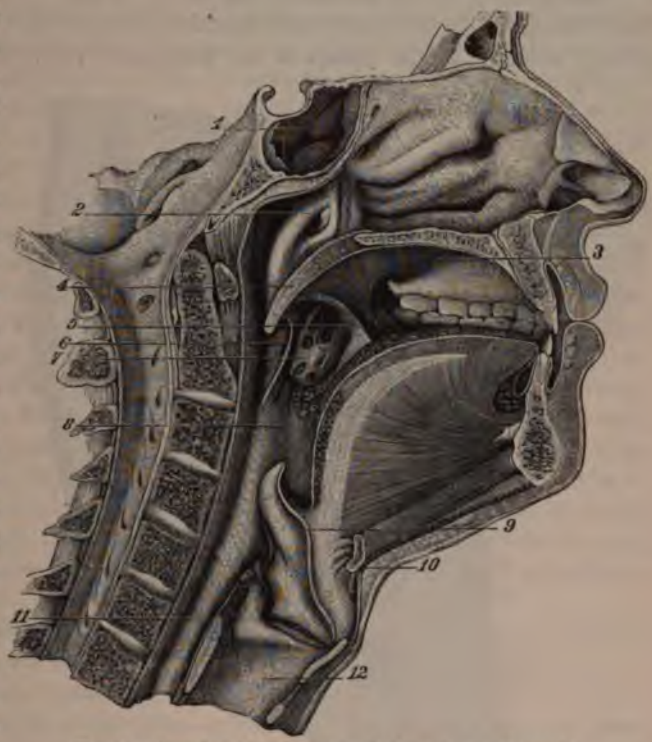

FIG. 55.—*Cavities of the mouth and pharynx, etc.* (Sappey).
Section, in the median line, of the face and the superior portion of the neck, designed to show the mouth in its relations to the nasal fossæ, the pharynx and the larynx: 1, sphenoidal sinuses; 2, internal orifice of the Eustachian tube; 3, palatine arch; 4, velum pendulum palati; 5, anterior pillar of the soft palate; 6, posterior pillar of the soft palate; 7, tonsil; 8, lingual portion of the cavity of the pharynx; 9, epiglottis; 10, section of the hyoid bone; 11, laryngeal portion of the cavity of the pharynx; 12, cavity of the larynx.

The anterior pillars of the fauces are formed by the palato-glossus muscle on either side and run obliquely downward and forward, the mucous membrane which covers them becoming continuous with the membrane over the base of the tongue. The posterior pillars are more closely approximated to each other than the anterior. They run obliquely downward and backward, their mucous membrane becoming continuous with the membrane covering the sides of the pharynx. Between the lower portion of the anterior and posterior pillars, are the tonsils; and in the substance of and beneath the mucous membrane of the palate and pharynx, are small glands, which have already been described.

In Fig. 55, are shown the cavities of the mouth and pharynx with their relations to the nares and the larynx.

The isthmus of the fauces, or the strait through which the food passes from the mouth to the pharynx, is bounded above, by the soft palate and the uvula; laterally, by the pillars of the palate and the tonsils; and below, by the base of the tongue.

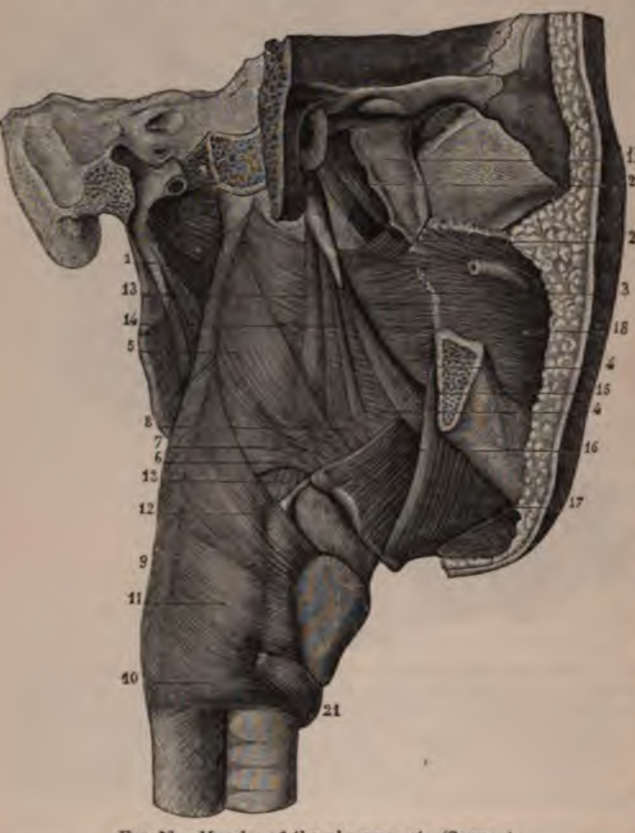


FIG. 56.—*Muscles of the pharynx, etc.* (Sappey).
1, 2, 3, 4, 4, superior constrictor; 5, 6, 7, 8, middle constrictor; 9, 10, 11, 12, inferior constrictor; 13, 13, stylo-pharyngeus; 14, stylo-hyoid muscle; 15, stylo-glossus; 16, hyo-glossus; 17, mylo-hyoid muscle; 18, buccinator muscle; 19, tensor palati; 20, levator palati.

The openings into the pharynx above are the posterior nares and the orifices of the Eustachian tubes. Below, are the openings of the œsophagus and of the larynx.

The muscles of the pharynx are the superior constrictor, the stylo-pharyngeus, the middle constrictor and the inferior constrictor; and it is easy to see, from the situation of these muscles, which is shown in Fig. 56, how, by their successive action from above downward, the food is passed into the œsophagus.

The muscles which form the fleshy portions of the soft palate are likewise important in deglutition. These are the levator palati, the tensor palati, the palato-glossus and the palato-pharyngeus. The azygos uvulæ, which forms the fleshy portion of the uvula, has no marked or important action in deglutition.

The mucous membrane of the pharynx, aside from the various glands situated beneath it and in its substance, which have already been described, presents some peculiarities, which are interesting more from an anatomical than a physiological point of view. In the superior portion, which forms a cuboidal cavity just behind the posterior nares, the membrane is darker and much richer in blood-vessels than in other parts. Its surface is smooth and provided with ciliated, columnar epithelium, like that which covers the membrane of the posterior nares. Laterally, below the level of the opening of the Eustachian tubes, and posteriorly, at the point where it becomes vertical, the mucous membrane abruptly changes its character. The epithelial covering is here composed of flattened cells, similar to those which cover the mucous membrane of the œsophagus. The membrane is also paler and less vascular. It is provided with papillæ, some of which are simple, conical elevations, while others present two to six conical processes with a single base. These papillæ are rather thinly distributed over all of that portion of the mucous surface which is covered with flattened epithelium.

The contractions of the muscular walls of the pharynx force the alimentary bolus into the œsophagus, a tube possessed of thick, muscular walls, extending to the stomach. The œsophagus is about nine inches (23 centimetres) in length. It is cylindrical and is slightly constricted at its superior and inferior extremities. Its upper extremity is in the median line, behind the lower border of the cricoid cartilage and opposite the fifth cervical vertebra. At first, as it descends, it passes a little to the left of the cervical vertebræ. It then passes from left to right from the fourth or fifth to the ninth dorsal vertebra, to give place to the aorta. It finally passes a little to the left again, and from behind forward, to its opening into the stomach. In its passage through the diaphragm, it is surrounded by muscular fibres, so that when this muscle is contracted in inspiration, its action has a tendency to close the opening.

The coats of the œsophagus are two in number, unless there be included, as a third coat, the fibrous tissue which attaches the mucous membrane to the subjacent muscular tissue.

The external coat is composed of an external longitudinal, and an internal circular or transverse layer of muscular fibres. In the superior portion, the longitudinal fibres are arranged in three distinct fasciculi; one in front, which passes downward from the posterior surface of the cricoid cartilage, and one on either side, extending from the inferior constrictors of the pharynx. As the fibres descend, the fasciculi become less distinct and are finally blended into a uniform layer. The circular layer is somewhat thinner than the external layer. Its fibres are transverse near the superior and inferior extremities of the tube and are somewhat oblique in the intermediate portion. The muscular coat is $\frac{1}{50}$ to $\frac{1}{12}$ of an inch (0·5 to 2·1 mm.) in thickness.

In the upper third of the œsophagus, the muscular fibres are exclusively of the red or striated variety, with some anastomosing bundles; but lower down, there is a mixture of non-striated fibres, which appear first in the circular layer. These latter fibres become gradually more abundant, until, in the lower fourth, they largely predominate. A few striated fibres, however, are found as low down as the diaphragm.

The mucous membrane of the œsophagus is attached to the muscular tissue by a dense, fibrous layer. It is quite vascular and reddish above, but gradually becomes paler in the inferior portion. The mucous membrane is ordinarily thrown into longitudinal folds, which are obliterated when the tube is distended. Its epithelium is thick, of the squamous variety, and is continuous with and similar to the covering of the lower portion of the pharynx. It is provided with papillæ of the same structure as those found in the pharynx, the conical variety predominating. Small, racemose glands are found throughout the tube, forming, by their aggregation at the lower extremity just before it opens into the stomach, a glandular ring.

*Mechanism of Deglutition.*—For convenience of description, physiologists have generally divided the process of deglutition into three periods. The first period is occupied by the passage of the alimentary bolus backward to the isthmus of the fauces. This may appropriately be considered as a distinct period, because the movements are effected by the action of muscles under the control of the will. The second period is occupied by the passage of the food from the isthmus of the fauces, through the pharynx, into the upper part of the œsophagus. The third period is occupied by the passage of the food through the œsophagus into the stomach.

In the first period the tongue is the important agent. At the beginning of this period, the mouth is closed and the tongue becomes slightly increased in width, and with the alimentary bolus behind it, is pressed from before backward against the roof of the mouth. The act of swallowing is always performed with difficulty when the mouth is not completely closed; for the tongue, from its attachments, must follow, to a certain extent, the movements of the lower jaw. The first part of the first period of deglutition, therefore, is simple; but when the food has passed beyond the hard palate, it comes in contact with the hanging velum, and the muscles are brought into action which render this membrane tense and oppose it in a certain degree to the backward movement of the base of the tongue. This is effected by the action of the tensor-palati and the palato-glossus. The moderate tension of the soft palate admits of its being applied to the smaller morsels, while the opening is dilated somewhat forcibly by masses of greater size.

It is easy to see, in analyzing the first period of deglutition, that liquids and the softer articles of food are assisted in their passage to the isthmus of the fauces by a slight suction force. This is effected by the action of the muscles of the tongue, elevating the sides and depressing the centre of the dorsum, while the soft palate is applied to the base.

The importance of the movements of the tongue during the first period of deglutition is shown by experiments on the inferior animals and by cases of loss of this organ in the human subject. In the case of a young girl, reported by De Jussieu (1718), in which there was congenital absence of the tongue, deglutition was impossible until the food had been pushed with the finger far back into the mouth. In cases of amputation of the tongue, a portion of its base generally remains, which is sufficient to press against the palate and thus act in the first period of deglutition.

The movements in the first period of deglutition are under the control of the will but are generally automatic. When the food has been thoroughly masticated, it requires an effort to prevent the act of swallowing. In this respect, the movements are like the acts of respiration, except that the imperative necessity of air in the system must, in a short time, overcome any voluntary effort by which respiration has been arrested.

The second period of deglutition involves more complex and important muscular action than the first. By a rapid succession of movements, the food is made to pass through the pharynx into the œsophagus. The movements are then entirely beyond the control of the will and belong to the kind called reflex. After the alimentary mass has passed beyond the isthmus of the fauces, it is easy to observe a sudden and peculiar movement of elevation of the larynx, by the action of muscles which usually depress the lower jaw, but which are now acting from this bone as the fixed point. The muscles which produce this movement act chiefly upon the hyoid bone. They are the digastric (particularly the anterior belly), the mylo-hyoid, the genio-hyoid, the stylo-hyoid and some of the fibres of the genio-glossus. It is probable, also, that the thyro-hyoid acts at this time to draw the larynx toward the hyoid bone. With this elevation of the larynx, there is necessarily an elevation of the anterior and inferior portions of the pharynx, which are, as it were, slipped under the alimentary bolus as it is held by the constrictors of the isthmus of the fauces.

Contraction of the constrictor muscles of the pharynx takes place almost simultaneously with the movement of elevation; and the superior constrictor is so situated as to grasp the morsel of food, and with it the soft palate. The muscles, the constrictors acting from the median raphe, draw up the anterior and inferior walls of the pharynx and pass the food rapidly into the upper part of the œsophagus. All these complex movements are accomplished with great rapidity, and the larynx and pharynx are then returned to their original position.

*Protection of the Posterior Nares during the Second Period of Deglutition.*—When the act of deglutition is performed with regularity, no portion of the liquids and solids swallowed ever finds its way into the air-passages. The entrance of foreign substances into the posterior nares is prevented in part by the action of the superior constrictors of the pharynx, which embrace, during their contraction, not only the alimentary mass, but the velum pendulum palati itself, and in part, also, by contraction of the muscles which form the posterior pillars of the soft palate.

During the first part of the second period of deglutition, the soft palate is slightly raised, being pressed upward by the morsel of food. This fact has been observed in cases in which the parts have been exposed by surgical operations, and its mechanism has also been observed in the human subject, by Bidder and by Kobelt.

While the food is passing through the pharynx, the palato-pharyngeal muscles, which form the posterior pillars of the soft palate, are in a condition of contraction by which the edges of the pillars are nearly approximated, forming, with the uvula between them, almost a complete diaphragm between the postero-superior and the antero-inferior parts of the pharynx. This, with the application of the posterior wall of the pharynx to the superior face of the soft palate, completes the protection of the posterior openings of the nasal fossæ.

*Protection of the Opening of the Larynx and Uses of the Epiglottis in Deglutition.*—The entrance of the smallest quantity of solid or liquid foreign matter into the larynx produces a violent cough. This accident is of not infrequent occurrence, especially when an act of inspiration is inadvertently performed while solids or liquids are in the pharynx. During inspiration, the glottis is opened, and at that time only can a substance of any considerable size find its way into the respiratory passages. Respiration is interrupted, however, during each and every act of deglutition; and there can, therefore, be hardly any tendency at that time to the entrance of foreign substances into the larynx. During a regular act of swallowing, nothing can find its way into the respiratory passages, so complete is the protection of the larynx during the period when the food passes through the pharynx into the œsophagus.

It is evident, from the anatomy of the parts and the necessary results of the contractions of the muscles of deglutition, that while the food is passing through the pharynx, the larynx, by its elevation, passes under the tongue as it moves backward, and the soft base of this organ is, as it were, moulded over the glottis. With the parts removed from the human subject or from one of the inferior animals, the natural movements of the tongue and larynx can be imitated, and it is seen that they must be sufficient to protect the larynx from the entrance of solid or semi-solid particles of food, particularly when it is remembered how the alimentary particles are agglutinated by the saliva and how easy their passage becomes over the membrane coated with mucus. It is impossible, also, for the muscles of the pharynx to contract without drawing together the sides of the larynx, to which they are attached, and assisting to close the glottis. At the same time, as the movements of respiration are arrested during deglutition, the lips of the glottis fall together, as they always do except in inspiration. In addition to this passive and incomplete approximation of the vocal chords, it has repeatedly been observed that the lips of the glottis are accurately and firmly closed during each act of deglutition.

Longet justly attached great importance to the acute sensibility of the top of the larynx in preventing the entrance of foreign substances. His experiments of dividing all the nervous filaments distributed to the intrinsic muscles show that their action is not essential; but after division of the superior laryngeal—the nerve which gives sensibility to the parts—he found that liquids occasionally passed in small quantity into the trachea.

With reference to the action of the epiglottis in contributing to the protection of the larynx during the second period of deglutition, observations on the human subject only are to be relied upon. Such observations, in cases of loss of the epiglottis especially, show that this part is necessary to the complete protection of the larynx. While loss of the epiglottis may not interfere always with the perfect deglutition of solids, and even of liquids, particles of food and liquids frequently find their way into the larynx, and deglutition is often effected with difficulty, showing that complete protection of the larynx at all times, does not exist unless the epiglottis be intact.

To appreciate the mechanism by which the opening of the larynx is protected during the deglutition of solids and liquids, one has only to carefully follow the articles as they pass over the inclined plane formed by the back of the tongue and the anterior and inferior part of the pharynx. As the food is making this passage in obedience to the contraction of the muscles which carry the tongue backward, draw up the larynx and constrict the pharynx, the soft base of the tongue and the upper part of the larynx are applied to each other, with the epiglottis, which is now inclined backward, between them; at the same time the glottis is closed, in part by the action of the constrictor muscles attached to the sides of the thyroid cartilages, and in part by the action of the intrinsic muscles. If the food be tolerably consistent and in the form of a single bolus, it slips easily from the back of the tongue along the membrane covering the anterior and inferior part of the pharynx; but if it be liquid or of soft consistence, a portion takes this course, while another portion passes over the epiglottis, being directed by it into the two grooves by the side of the larynx. It is by these means, together with those by which the posterior nares are protected, that all solids and liquids are passed into the œsophagus, and the second period of deglutition is safely accomplished.

The third period of deglutition is the most simple of all. It merely involves contractions of the muscular walls of the œsophagus, by which the food is passed into the stomach. The longitudinal fibres shorten the tube and slip the mucous membrane, lubricated by its glairy secretion, above the bolus; while the circular fibres, by a progressive peristaltic contraction from above downward, propel the food into the stomach. In experiments on the lower animals, it has been observed that while the peristaltic contractions of the upper two-thirds of the tube is immediately followed by a relaxation, which continues till the next act of deglutition, the lower third remains contracted generally for about thirty seconds after the passage of the food into the stomach. During its contraction, this part of the œsophagus is hard, like a cord firmly stretched. This is followed by relaxation; and alternate contraction and relaxation continue, even when the stomach is empty, although, during digestion, the contractions are frequent in proportion to the quantity of food in the stomach. The contraction is always increased by pressing the stomach and attempting to pass some of its contents into the œsophagus (Magendie). This provision is important in preventing regurgitation of the contents of the stomach, especially when the organ is exposed to pressure, as in urination or defecation.

An approximate estimate of the duration of the acts of deglutition is given in the following quotation from Landois:

"According to Meltzer and Kronecker, the duration of deglutition in the mouth is 0·3 sec.; then the constrictors of the pharynx contract 0·9 sec.; afterward, the upper part of the œsophagus; then after 1·8 sec. the middle; and after another 3 sec. the lower constrictor. The closure of the cardia, after the entrance of the bolus into the stomach, is the final act in the total series of movements."

The entire process of deglutition, therefore, occupies about six seconds.

The muscular movements which take place during all the periods of deglutition are peculiar. The first act is generally automatic, but it is under the control of the will. The second act is involuntary when once begun, but it may be excited by the voluntary passage of solids or liquids beyond the velum pendulum palati. It is impossible to perform the second act of deglutition unless there be some article, either solid or liquid, in the pharynx. It is easy to make three or four successful efforts consecutively, in which there is elevation of the larynx, with all the other characteristic movements; but a little attention will show that with each act a small quantity of saliva is swallowed. When the efforts have been frequently repeated, the movements become impossible, until time enough has elapsed between them for the saliva to collect.

All the movements of deglutition, except those of the first period, must be regarded as reflex, depending upon an impression made upon the afferent nerves distributed to the mucous membrane of the pharynx and œsophagus.

The position of the body has little to do with the facility with which deglutition is effected. Liquids or solids may be swallowed indifferently in all postures. Bérard saw a juggler pass an entire bottle of wine from the mouth to the stomach, while standing on his head. The same feat was accomplished with apparent ease, by a juggler who drank three glasses of beer while standing on his hands in the inverted posture (Flint).

*Deglutition of Air.*—In his essay on the mechanism of vomiting, Magendie stated that as soon as nausea occurred the stomach began to fill with air, so that before vomiting occurred, the organ became tripled in size. Magendie showed, fathermore, that the air entered the stomach by the œsophagus, for the distention occurred when the pylorus was ligated. In a subsequent memoir, the question of the deglutition of air, aside from the small quantity which is incorporated with the food during mastication and insalivation, was farther investigated. It was found that some persons had the faculty of swallowing air, and by practice, Magendie himself was able to acquire it, although it occasioned such distress that it was discontinued. Out of a hundred students of medicine, eight or ten were found able to swallow air.

It is not very uncommon to find persons who have gradually acquired the habit of swallowing air, in order to relieve uncomfortable sensations in the stomach; and when confirmed, it occasions persistent disorder in digestion. Quite a number of cases of this kind were reported by Magendie, and in several it was carried to such an extent as to produce great distention of the abdomen. A curious case of habitual air-swallowing was observed by the late Dr. Austin Flint and is reported in his work on the Practice of Medicine.

# CHAPTER VIII.

## *GASTRIC DIGESTION.*

**Physiological anatomy of the stomach—Glands of the stomach—Closed follicles—Gastric juice—Gastric fistula in the human subject in the case of St. Martin—Secretion of the gastric juice—Properties and composition of gastric juice—Action of the gastric juice in digestion—Peptones—Action of the gastric juice upon fats, sugars and amylaceous substances—Duration of gastric digestion—Conditions which influence gastric digestion—Movements of the stomach.**

### PHYSIOLOGICAL ANATOMY OF THE STOMACH.

THE stomach serves the double purpose of a receptacle for the food and an organ in which certain important digestive processes take place. It is situated in the upper part of the abdominal cavity and is held in place by folds of the peritoneum and by the œsophagus. Its form is not easily described. It has been compared to a bagpipe, which it resembles somewhat, when moderately distended. When empty, it is flattened, and in many parts its opposite walls are in contact. When moderately distended, its length is thirteen to fifteen inches (33 to 38 centimetres), its greatest diameter, about five inches (12·7 centimetres), and its capacity, one hundred and seventy-five cubic inches (2,868 c. c.), or about five pints. The parts usually noted in anatomical descriptions are the following: a greater and a lesser curvature; a greater and a lesser pouch; a cardiac, or œsophageal opening; a pyloric opening, which leads to the intestinal canal. The great pouch is sometimes called the fundus.

The coats of the stomach are three in number; the peritoneal, muscular and mucous. By some anatomists the fibrous tissue which unites the mucous to the muscular coat is regarded as a distinct covering and is called the fibrous coat.

*Peritoneal Coat.*—This is simply a layer of peritoneum, similar in structure to the membrane which covers the other abdominal viscera. It is a reflection of the membrane which lines the general abdominal cavity, which, on the viscera, is somewhat thinner than it is on the walls of the cavity. Over the stomach the peritoneum is $\frac{1}{300}$ to $\frac{1}{200}$ of an inch (83 to 125 $\mu$) in thickness. It is a serous membrane and consists of ordinary fibrous tissue with a considerable number of elastic fibres. It is closely adherent to the subjacent muscular coat and is not very abundantly supplied with blood-vessels and nerves. Lymphatics have been demonstrated only in the subserous structure. The surface of the peritoneum is everywhere covered with regularly polygonal cells of pavement endothelium, closely adherent to each other and presenting a perfectly smooth surface which is moistened with a small quantity of liquid. An important office of this membrane is to present a smooth surface covering the abdominal parietes and viscera, so as to allow free movements of the organs over each other and against the walls of the abdomen.

*Muscular Coat.*—Throughout the alimentary canal, from the cardiac opening of the stomach to the anus, the muscular fibres forming the middle coat are of the non-striated variety. These fibres, called sometimes muscular fibre-cells, are very pale, with faint outlines, fusiform or spindle-shaped, and contain each an oval, longitudinal nucleus. They are closely adherent by their sides, and are so arranged as to dovetail into each other, forming sheets of greater or less thickness, depending upon the number of their layers. The muscular coat of the stomach varies in thickness in different animals. In the human subject, it is thickest in the region of the pylorus and is thinnest at the fundus. Its average thickness is about $\frac{1}{25}$ of an inch (1 mm.). In the pylorus its thickness is $\frac{1}{16}$ to $\frac{1}{12}$ of an inch (1·6 to 2·1 mm.), and in the fundus, $\frac{1}{50}$ to $\frac{1}{36}$ of an inch (0·5 to 0·7 mm.).

The muscular fibres exist in the stomach in two principal layers; an external longitudinal layer and an internal circular layer, with a third layer of oblique fibres extending over the great pouch only, which is internal to the circular layer. The longitudinal fibres are continued from the œsophagus and are most marked over the lesser curvature. They are not continued very distinctly over the rest of the stomach. The circular and oblique fibres are best seen with the organ everted and the mucous membrane carefully removed. The circular layer is not very distinct to the left of the cardiac opening, over the great pouch. Toward the pylorus, the layers of fibres are thicker, and at the opening into the duodenum, they form a powerful muscular ring, which is sometimes called the sphincter of the pylorus, or the pyloric muscle. At this point they project considerably into the interior of the organ and cease abruptly at the opening into the duodenum, so as to form a sort of valve, presenting, when contracted, a flat surface looking toward the

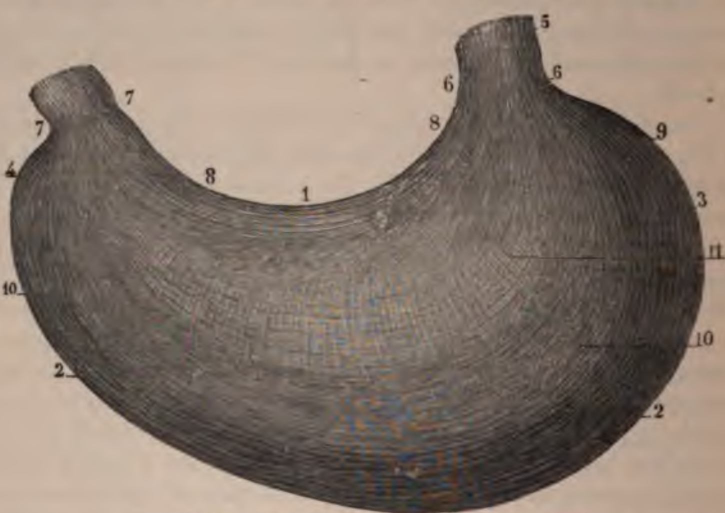


FIG. 57.—*Longitudinal fibres of the stomach* (Sappey).

1, lesser curvature ; 2, 2, greater curvature ; 3, greater pouch ; 4, lesser pouch ; 5, 6, 6, lower end of the œsophagus ; 7, 7, pylorus ; 8, 8, longitudinal fibres at the lesser curvature ; 9, fibres extending over the greater curvature ; 10, 10, a very thin layer of longitudinal fibres over the anterior surface of the stomach ; 11, circular fibres seen through the thin layer of longitudinal fibres.

intestine. The oblique layer takes the place, in great part, of the circular fibres, over the great pouch. It extends obliquely over the fundus from left to right and ceases at a distinct line extending from the left margin of the œsophagus to about the junction of the middle with the last third of the great curvature. At about the line where the oblique layer of fibres ceases the stomach becomes constricted during the movements which are incident to digestion, dividing the organ into tolerably distinct compartments.

The blood-vessels of the muscular coat are quite abundant and are arranged in a peculiar, rectangular net-work, which they always present in the non-

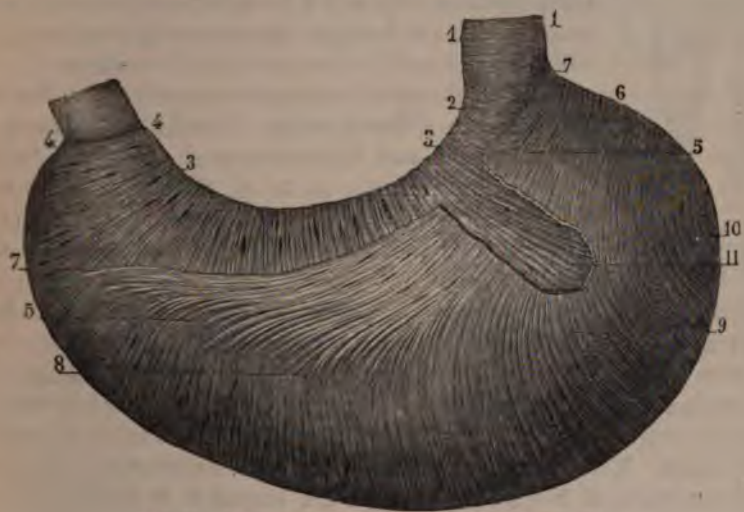


FIG. 58.—*Fibres seen with the stomach everted* (Sappey).

1, 1, œsophagus; 2, circular fibres at the œsophageal opening; 3, 3, circular fibres at the lesser curvature; 4, 4, circular fibres at the pylorus; 5, 5, 6, 7, 8, oblique fibres; 9, 10, fibres of this layer covering the greater pouch; 11, portion of the stomach from which these fibres have been removed to show the subjacent circular fibres.

striated muscular tissue. The nerves come from the pneumogastrics and the sympathetic system and are demonstrated with difficulty.

*Mucous Coat.*—The mucous membrane of the stomach is soft and velvety in appearance and of a reddish-gray color. It is loosely attached to the submucous muscular tissue and is thrown into large, longitudinal folds, which become effaced as the organ is distended. If the mucous membrane be stretched or if the stomach be everted and distended and the mucus be gently removed under a stream of water, the membrane will be found marked with polygonal pits or depressions, enclosed by ridges, which, in some parts of the organ, are quite regular. These are best seen with


FIG. 59.—*Pits in the mucous membrane of the stomach, and orifices of the glands; magnified 20 diameters* (Sappey).

1, 1, 1, 2, 2, 2, 3, pits of different sizes; 4, 5, orifices of the gastric glands.

the aid of a simple lens, as many of them are quite small. The diameter of the pits is very variable, but the average is about $\frac{1}{200}$ of an inch (0·125 mm.). This appearance is not distinct toward the pylorus; the membrane here presenting irregular, conical projections and well marked villi resembling those found in the small intestine. The surface of the mucous membrane is covered with columnar or prismoidal epithelium, the cells being tolerably regular in shape, each with a clear nucleus and a distinct nucleolus. According to Landois, these cells, which he calls "mucus-secreting goblet-cells," have a clear portion occupying their outer half, which is open and discharges a viscid secretion.

FIG. 60.—*Goblet-cells from the stomach* (Landois).

The thickness of the mucous membrane of the stomach varies in different parts. Usually it is thinnest near the œsophagus and thickest near the pylorus. Its thinnest portion measures $\frac{1}{75}$ to $\frac{1}{50}$ of an inch (0·34 to 0·5 mm.); its thickest portion, $\frac{1}{16}$ to $\frac{1}{12}$ of an inch (1·6 to 2·1 mm.), and the intermediate portion, about $\frac{1}{25}$ of an inch (1 mm.).

*Glands of the Stomach.*—Extending from the bottoms of the pits in the mucous membrane of the stomach to the submucous connective tissue, are large numbers of glands. These generally are arranged in tolerably distinct groups, surrounded by fibrous tissue, each group belonging to one of the polygonal depressions. The tissue which connects the tubes is dense but not abundant. There are marked differences in the anatomy of the glands in different parts of the stomach, which are supposed to correspond with differences in the uses of various parts of the mucous membrane. There are, indeed, two distinct varieties of glands; the peptic glands, which secrete pepsine, or an organic substance that is readily changed into pepsine, and the acid-glands, which are supposed to secrete free hydrochloric acid. The peptic glands are most abundant in the pyloric portion of the stomach and around the cardiac opening. The so-called acid-glands are found throughout the mucous membrane, especially in the greater pouch. The secretion in the pyloric portion of the stomach is not acid at any time, while the secretion in the greater pouch, during digestion, is always strongly acid. The difference in the action of these two kinds of glands is supposed to depend upon differences in the secreting cells.

The pyloric glands are lined by cells which may be called peptic cells (the chief-cells of German writers), conoidal or cuboidal in form, and relatively clear, especially during the intervals of digestion. Similar cells are found, in connection with the so-called acid-cells (parietal cells) in the secreting portion of the glands of the greater pouch.

The acid-glands are found throughout the stomach, except near the pylorus. The secreting portion of these glands contains peptic cells, but near the tubular membrane are rounded cells, larger than the peptic cells, darker and more granular, which are the acid, or parietal cells. These are strongly stained when treated with osmic acid (Nussbaum). It is probable that the so-called acid-glands secrete pepsine as well as an acid, while the pyloric glands secrete pepsine but no acid. According to the views just stated, in the glands of the greater pouch, the acid is secreted by the rounded acid-cells while the pepsine is secreted by cells (peptic cells) similar to those which line the secreting portion of the pyloric glands. During the intervals of digestion, pepsine is in process of formation by the peptic cells, and no acid is produced; but acid begins to be secreted soon after food is received into the stomach. It is now thought that the peptic cells do not produce pepsine directly, but a substance sometimes called zymogen, but more properly propepsine or pepsinogen, which is changed into true pepsine by the action of hydrochloric acid.

There is some confusion among writers with regard to the names of the different kinds of secreting cells of the stomach, the acid-cells being frequently described as "peptic cells." It seems proper, however, to call the

FIG. 61.—*Glands of the greater pouch of the stomach* (Heidenhain).

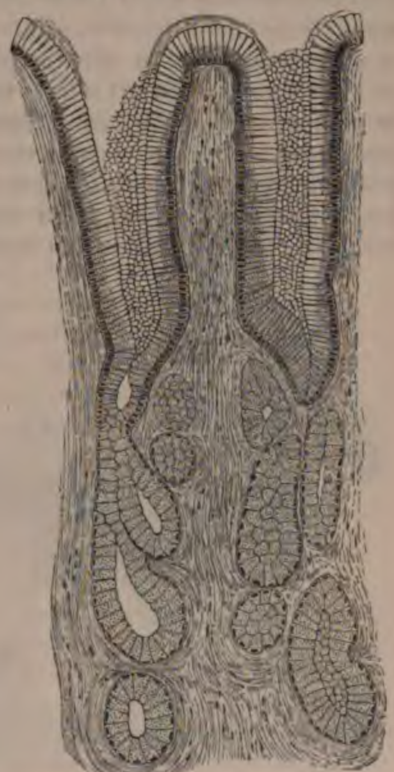

FIG. 62.—*Pyloric glands* (Ebstein).

cells which produce pepsine, peptic cells, and the cells that are supposed to produce acid, acid-cells.

The glands of the stomach have an excretory portion and a secreting portion, the latter presenting several branches. The excretory portion is lined by cells like those found on the surface of the mucous membrane.

The secreting portion is lined by the peptic and the acid-cells already described. In Fig. 61 the darker cells are the acid-cells, and the lighter cells, the peptic cells. In Fig. 62 the secreting portion contains peptic cells only.

*Closed Follicles.*—In the substance of the mucous membrane, between the tubes and near their cæcal extremities, are occasionally found closed follicles, like the solitary glands and patches of Peyer of the intestines. These are not always present in the adult but are generally found in children. They are usually most abundant over the greater curvature, though they may be found in other situations. In their anatomy they are identical with the closed follicles of the intestines, and they do not demand special consideration in this connection.

*Gastric Juice.*—The observations of Beaumont upon Alexis St. Martin, the Canadian who had a large fistulous opening into the stomach, gave the first definite knowledge of the most important of the physiological properties of the gastric juice. St. Martin, the subject of these observations, received a gunshot wound in the left side, at the age of eighteen years, being at the time of good constitution and in perfect health. He slowly recovered from the injury, and after three years, having regained his health, was made the subject of a great number and variety of experiments. Although the general health had been restored, there remained a perforation into the stomach, irregularly circular in form and nearly an inch (2·5 centimetres) in diameter. This opening was closed by a protrusion of the mucous membrane in the form of a valve, which could readily be depressed by the finger so as to expose the interior of the stomach.

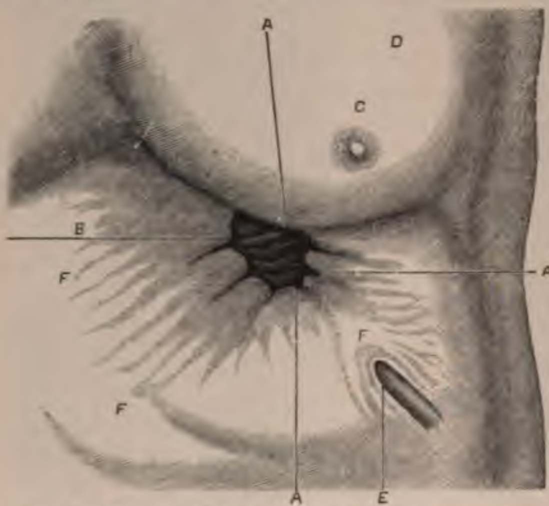


FIG. 63.—*Gastric fistula in the case of St. Martin* (Beaumont). A, A, A, B, borders of the opening into the stomach; C, left nipple; D, chest; E, cicatrices from the wound made for the removal of a piece of cartilage; F, F, F, cicatrices of the original wound.

From May, 1825, until August of the same year, St. Martin was under the observation of Beaumont. At the end of that time he was lost sight of for four years. He then came again under the observation of Beaumont and continued in his service, doing the work of a servant, until March, 1831. After this he was under observation from time to time until 1836, always enjoying perfect health, with good digestion. The last published observations made upon this case were in 1856.

The following was the method employed by Beaumont in extracting the gastric juice: The subject was placed on the right side in the recumbent posture, the valve was depressed within the aperture, and a gum-elastic tube, of the size of a large quill, was passed into the stomach to the extent of five to six inches (12 to 15 centimetres). On turning him upon the left side until the opening became dependent, the stimulation of the tube caused the secretion to flow, sometimes in drops and sometimes in a small stream.

Since the publication of Beaumont's experiments, many observations have been made upon animals in which a permanent gastric fistula had been established. In these experiments the dog is most frequently used, as in this animal the operation usually is successful. The animals operated upon by Bassow, who was the first to establish a gastric fistula (1842), were merely objects of curiosity; but Blondlot (1843) and others fixed a tube in the stomach, collected the juice and made important observations with regard to its action in digestion. Most experimenters follow the method employed by Blondlot and Bernard, making the opening in the abdomen in the median line, a little below the ensiform cartilage.

Having established a permanent fistula into the stomach, after the wound has cicatrized around the canula, the animal suffers no inconvenience and may serve indefinitely for experiments on the gastric juice. In some experiments, the flow of gastric juice has been excited by the introduction into the stomach, of pieces of tendon or hard, indigestible articles, on the ground that the fluid taken from the fistula, under these conditions, is unmixed with the products of gastric digestion; but it has been shown that the quantity and character of the secretion are influenced by the nature of the stimulus, and it is proper, therefore, to excite the action of the stomach by articles which are relished by the animal. For this purpose, lean meat may be given, cut into pieces so small that they will be swallowed entire, and first thrown into boiling water so that their exterior may become somewhat hardened. The cork is then removed from the tube, which is freed from mucus etc., when the gastric juice will begin to flow, sometimes immediately and sometimes in four or five minutes after the food has been taken. It flows in clear drops or in a small stream for about fifteen minutes, nearly free from the products of digestion. At the end of this time it is generally accompanied with grumous matter, and the experiment should be concluded if it be desired simply to obtain the pure secretion. In fifteen minutes, two to three ounces (60 to 90 c.c.) of fluid may be obtained from a good-sized dog, which, when filtered, is perfectly clear; and this operation may be repeated three or four times a

FIG. 64.—*Dog with a gastric fistula* (Béclard).

week without interfering with the character of the secretion or injuring the health of the animal.

Although instances of gastric fistula in the human subject had been reported before the case of St. Martin and have been observed since that time, the remarkably healthy condition of the subject and the extended experiments of Beaumont have rendered this case memorable in the history of physiology. This is the only instance on record, in which pure, normal gastric juice has been obtained from the human subject; and it has served as the standard for comparison for subsequent experiments on the inferior animals.

Artificial gastric juice, prepared by extracting the active principle from the mucous membrane of the stomach of different animals and adding hydrochloric acid, is useful in observations with regard to the chemistry of the peculiar ferment, but fluids prepared in this way are not absolutely identical with the natural secretion. Extracts of the mucous membrane were made by Eberle (1834), Von Wittich, Brücke and many others.

*Secretion of the Gastric Juice.*—According to Beaumont, during the intervals of digestion, the mucous membrane is comparatively pale, "and is constantly covered with a very thin, transparent, viscid mucus, lining the whole interior of the organ." On the application of any irritation, or better, on the introduction of food, the membrane changes its appearance. It becomes red and turgid with blood; small pellucid points begin to appear in various parts, which are drops of gastric juice; and these gradually increase in size until the fluid trickles down the sides in small streams. The membrane is now invariably of a strongly acid reaction, while at other times it is either neutral or faintly alkaline. The thin, watery fluid thus produced is the true gastric juice. Although the stomach may contain a clear fluid at other times, this secretion generally is abnormal. It is but slightly acid and does not possess the characteristic properties of the natural secretion. It has been shown by Beaumont, and his observations have been repeatedly confirmed by experiments on the inferior animals, that the gastric juice is secreted in greatest quantity and possesses the most powerful solvent properties, when food has been introduced into the stomach by the natural process of deglutition. The stimulation of the mucous membrane is then general, and secretion takes place from the entire surface capable of producing the fluid. When any foreign substance, as the gum-elastic tube used in collecting the juice, is introduced, the stimulation is local, and the flow of fluid is comparatively slight. It has been also observed that the quantity immediately secreted on the introduction of food, after a long fast, is always much greater than when food has been taken after the ordinary interval.

While natural food is undoubtedly the proper stimulus for the stomach, and while, in normal digestion, the quantity of gastric juice is perfectly adapted to the work it has to perform, it has been noted that savory and highly seasoned articles generally produce a more abundant secretion than those which are comparatively insipid. An abundant secretion is likewise excited by some of the vegetable bitters.

Impressions made on the nerves of gustation have a marked influence in exciting the action of the mucous membrane of the stomach. Blondlot found that sugar, introduced into the stomach of a dog by a fistula, produced a flow of juice much less abundant than when the same quantity was taken by the mouth. To convince himself that this did not depend upon the want of admixture with the alkaline saliva, he mixed the sugar with the saliva and passed it in by the fistula, when the same difference was observed. In some animals, particularly when they are very hungry, the sight and odor of food will excite secretion of gastric juice.

A febrile condition of the system, the depression resulting from an excess in eating and drinking, or even purely mental conditions, such as anger or fear, vitiate, diminish and sometimes entirely suppress secretion by the stomach. At some times, under these conditions, the mucous membrane becomes red and dry, and at others it is pale and moist. In the morbid conditions, drinks are immediately absorbed, but food remains undigested in the stomach for twenty-four to forty-eight hours (Beaumont).

After the food has been in part liquefied and absorbed and in part reduced to a pultaceous consistence, the secretion of gastric juice ceases; the movements of the stomach having gradually forced that portion of the food which is but partially acted upon in this organ or is digested only in the small intestines out at the pylorus. The stomach is thus entirely emptied, the mucous membrane becomes pale, and its reaction loses its marked, acid character, becoming neutral or faintly alkaline.

*Quantity of Gastric Juice.*—The *data* for determining the quantity of gastric juice secreted in the twenty-four hours are so uncertain that it seems impossible to fix upon any estimate that can be accepted even as an approximation. Still, the quantity must be considerable, in view of the large quantity of alimentary matter which is acted upon in gastric digestion. It is probably not less than six pounds (2·72 kilos.) or more than fourteen pounds (6·35 kilos.). After this fluid has performed its office in digestion, it is immediately reabsorbed, and but a small quantity of the secretion exists in the stomach at any one time.

*Properties and Composition of Gastric Juice.*—The gastric juice is mixed in the stomach with more or less mucus secreted by the lining membrane. When drawn by a fistula, it generally contains particles of food, which have become triturated and partially disintegrated in the mouth, and is always mixed with a certain quantity of saliva, which is swallowed during the intervals of digestion as well as when the stomach is active. By adopting certain precautions, however, the fluid may be obtained nearly free from impurities, except the admixture of saliva. The juice taken from the stomach during the first moments of its secretion, and separated from mucus and foreign matters by filtration, is a clear fluid, of a faint yellowish or amber tint and possessing little or no viscidity. Its reaction is always strongly acid; and it is now a well-established fact that any fluid, secreted by the mucous membrane of the stomach, which is either alkaline or neutral, is not normal gastric juice.

The specific gravity of the gastric juice in the case of St. Martin, according to the observations of Beaumont and Silliman, was 1005; but later, F. G. Smith found it in one instance, 1008, and in another, 1009. There is every reason to suppose that the fluid, in the case of St. Martin, was perfectly normal, and 1005 to 1009 may be taken as the range of the specific gravity of the gastric juice in the human subject.

The gastric juice is described by Beaumont as inodorous, when taken directly from the stomach; but it has rather an aromatic and a not disagreeable odor when it has been kept for some time. It is a little saltish, and its taste is similar to that of "thin, mucilaginous water slightly acidulated with muriatic acid."

It has been found by Beaumont, in the human subject, and by those who have experimented on the gastric juice of the lower animals, that this fluid, if kept in a well stoppered bottle, will retain its chemical and physiological properties for an indefinite period. The only change which it undergoes is the formation of a pellicle, consisting of a vegetable, confervoid growth, upon the surface, some of which breaks up and falls to the bottom of the vessel, forming a whitish, flocculent sediment. In addition to this remarkable faculty of resisting putrefaction, putrefactive changes are arrested in decomposing animal substances, both when taken into the stomach and when exposed to the action of the gastric juice out of the body.

There are on record no minute quantitative analyses of the human gastric juice, except those by Schmidt, of the fluid from the stomach of a woman with gastric fistula; and in this case there is reason to suppose that the secretion was not normal. The analysis of the gastric juice of St. Martin by Berzelius was not minute. The analyses of Schmidt give less than six parts per thousand of solid matter, while Berzelius found more than twelve parts per thousand. In all the comparatively recent analyses, there have been found a free acid or acids, a peculiar organic matter, generally called pepsine, and various inorganic salts.

The following analysis by Bidder and Schmidt gives the mean of nine observations upon dogs:

COMPOSITION OF THE GASTRIC JUICE OF THE DOG (BIDDER AND SCHMIDT).

| | |
|---|---|
| Water | 973·062 |
| Ferment (pepsine) | 17·127 |
| Free hydrochloric acid | 3·050 |
| Potassium chloride | 1·125 |
| Sodium chloride | 2·507 |
| Calcium chloride | 0·624 |
| Ammonium chloride | 0·468 |
| Calcium phosphate | 1·729 |
| Magnesium phosphate | 0·226 |
| Ferric phosphate | 0·082 |
| | 1,000·000 |

In another series of three observations, in which the saliva was allowed to pass into the stomach, the proportion of free acid was 2·337, and the proportion of organic matter was somewhat increased.

*Organic Constituent of the Gastric Juice.*—Pepsine is an organic nitrogenized substance, which is peculiar to the gastric juice and essential to its digestive properties. When the gastric fluid was first obtained, even by the imperfect methods employed anterior to the observations of Beaumont and of Blondlot, an organic matter was spoken of as one of its constituents.

Experiments on artificial digestive fluids, by Eberle, Schwann and Müller, Wasmann and others, have demonstrated that acidulated extracts of the mucous membrane of the stomach contain an organic matter, first isolated by Wasmann, on which the solvent powers of these acid fluids seem to depend. Mialhe, who has obtained this substance in great purity by the process recommended by Vogel, described the following properties as characteristic of the organic matter in artificial gastric juice: Dried in thin slices on a plate of glass, it is in the form of small, grayish, translucent scales, with a faint and peculiar odor and a feebly bitter and nauseous taste. It is soluble in water and in a weak alcoholic mixture, but is insoluble in absolute alcohol. A solution of it is rendered somewhat turbid by a temperature of 212° Fahr. (100° C.), but it is not coagulated, although it loses its digestive properties. It is not affected by acids but is precipitated by tannin, creosote and a great number of metallic salts. This substance dissolved in water slightly acidulated possesses, in a very marked degree, the solvent properties of the gastric juice; but it has been found by Payen and Mialhe not to be so active as the substance extracted from the gastric juice itself, which is described by Payen, under the name of gasterase. In the abattoirs of Paris, Mialhe collected from the secreting stomachs of calves as they were killed, between six and ten pints (2·8 and 4·7 litres) of gastric juice; and from this he extracted the pure pepsine by the process recommended by Payen, which consists merely in one or two precipitations by alcohol. This substance he found to be identical with the substance obtained by Payen from the gastric juice of the dog. Its action upon albuminoid matters was precisely the same as that of pepsine extracted from artificial gastric juice, except that it was more powerful.

*Free Acid of the Gastric Juice.*.—The character of the free acid of the gastric juice has long been a question of uncertainty and dispute. In former editions of this work, the different views of chemists with regard to the nature of this acid were fully discussed. It may now be stated that almost all physiologists adopt the view that the gastric juice contains free hydrochloric acid, with possibly a very small quantity of lactic acid. It is admitted, however, that the degree of acidity of the gastric juice is variable, and that the normal acid may be replaced, without loss of the digestive properties of the fluid, by lactic, oxalic, acetic, formic, succinic, tartaric, citric, phosphoric, nitric or sulphuric acid.

*Saline Constituents of the Gastric Juice.*—It has been shown that artificial fluids containing the organic matter of the gastric juice and the proper proportion of free acid are endowed with all the digestive properties of the normal secretion from the stomach, and that these properties are rather impaired when an excess of its normal saline constituents is added or when the relation of the salts to the water is disturbed by concentration.

Boudault and Corvisart evaporated 6·76 oz. (200 c. c.) of the gastric juice of the dog to dryness and added to the residue, 1·69 oz. (50 c. c.) of water. They found that the fluid thus prepared, containing four times the normal proportion of saline constituents, did not possess by any means the energy of action on alimentary substances of the normal secretion. These facts have led physiologists to attach little importance to the saline constituents of the gastric juice, except sodium chloride, which is thought to be concerned in the production of hydrochloric acid.

*Action of the Gastric Juice in Digestion.*—Certain of the substances most readily attacked by the gastric juice are acted upon by weak, acid solutions containing no organic matter; but it is now well established that the presence of a peculiar organic matter is a condition indispensable to actual digestion. It has also been shown that fluids containing the organic constituent of the gastric juice have no digestive properties unless they also possess the proper degree of acidity; and it is as well settled that fluids containing acids alone have no action on albuminoids similar to that which takes place in digestion, and that when these substances are dissolved by them it is simply accidental.

The presence of any one particular acid does not seem essential to the digestive properties of the gastric juice, so long as the proper degree of acidity is preserved, and it is undoubtedly important that the normal acid can be replaced by other acids; for in case any salt were introduced into the stomach which would be decomposed by the acid of the gastric juice, digestion would be interfered with, unless the liberated acid could take its place. It can readily be appreciated that transient disturbances might occur from this cause, were the existence of any one acid indispensable to the digestive properties of the gastric juice; while if only a certain degree of acidity were required, this condition might be produced by any acid, either derived from the food or secreted by the stomach.

In studying the physiological action of the gastric juice, it must always be borne in mind that the general process of digestion is accomplished by the combined as well as the successive action of the different digestive fluids. The act should be viewed in its *ensemble*, rather than as a process consisting of several successive and distinct operations, in which different classes of alimentary matters are dissolved by distinct fluids. The food meets with the gastric juice, after having become impregnated with a large quantity of saliva; and it passes from the stomach to be acted upon by the intestinal fluids, having imbibed both saliva and gastric juice.

When the acts which take place in the mouth are properly performed, the following alimentary substances, comminuted by the action of the teeth and thoroughly insalivated, are taken into the stomach: muscular tissue, containing the muscular substance enveloped in its sarcolemma, blood-vessels, nerves, ordinary fibrous tissue holding the muscular fibres together, interstitial fat, and a small quantity of albuminoids and corpuscles from the blood, all combined with a considerable quantity of inorganic salts; albumen, sometimes unchanged, but generally in a more or less perfectly coagulated condition;

fatty matter, sometimes in the form of oil and sometimes enclosed in vesicles, constituting adipose tissue; gelatine and animal matters in a liquid form extracted from meats, as in soups; caseine, in its liquid form united with butter and salts in milk, and coagulated in connection with various other matters, in cheese; vegetable nitrogenized matters, of which gluten may be taken as the type; vegetable fats and oils; sugars, both from the animal and vegetable kingdoms, but chiefly from vegetables; the different varieties of amylaceous substances; and finally, organic acids and salts, derived chiefly from vegetables. These matters, particularly those from the vegetable kingdom, are united with more or less innutritious matter, such as cellulose. They are also seasoned with aromatic substances, condiments etc., which are not directly used in nutrition.

The various articles described as drinks are taken without any considerable admixture with the saliva. They embrace water and the various nutritious or stimulant infusions (including alcoholic beverages) with a small proportion of inorganic salts in solution.

*Action of the Gastric Juice upon Meats.*—There are three ways in which the action of the gastric juice upon the various articles of food may be studied. One is to subject them to the action of the pure fluid taken from the stomach, as was done by Beaumont, in the human subject, and by Blondlot and others, in experiments upon the inferior animals; another is to make use of properly prepared acidulated extracts of the mucous membrane of the stomach, which have been shown to have many of the properties of the gastric juice, differing mainly in activity; and another is to examine from time to time the contents of the stomach after food has been taken. By all of these methods of study it has been shown that the digestion of meat in the stomach is far from complete. The parts of the muscular structure most easily attacked are the fibrous tissue which holds the muscular fibres together, and the sarcolemma, or sheath of the fibres themselves. If the gastric juice of the dog be placed in a vessel with finely chopped lean meat and be kept in contact with it for a number of hours at about 100° Fahr. (37·78° C.), agitating the vessel occasionally so as to subject, as far as possible, every particle of the meat to its action, the filtered fluid will be found increased in density, its acidity diminished, and presenting all the evidences of having dissolved a considerable portion of the tissue. There always, however, will remain a certain portion which has not been dissolved. Its constitution is nevertheless materially changed; for it no longer possesses the ordinary character of muscular tissue, but easily breaks down between the fingers into a pultaceous mass. On subjecting this residue to microscopical examination, it is found not to contain any ordinary fibrous tissue; and the fibres of muscular tissue, although presenting the well marked and characteristic striæ, are broken into short pieces and possess very little tenacity. It is evidently only the muscular substance which remains; the connective tissue and the sarcolemma having been dissolved. These facts have been repeatedly noted, and even on adding fresh juice to the undigested matter, it is not dissolved to any considerable extent, the residue not being sensibly diminished in quantity, and the muscular substance always presenting its characteristic striæ, on microscopical examination. Bernard, in experiments with the gastric juice of different animals, found the fluid from the stomach of the rabbit or the horse much inferior, as regards the activity of its action upon meat, to the gastric juice of the dog.

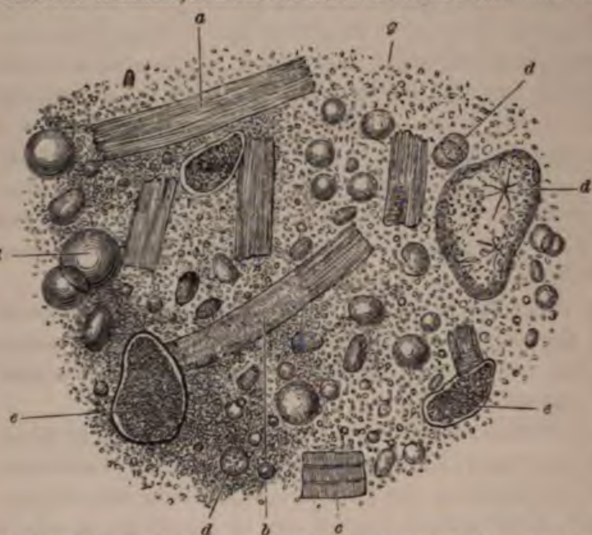


*Fig. 65.—Matters taken from the pyloric portion of the stomach of a dog during digestion of mixed food* (Bernard).

*a*, disintegrated muscular fibres, the striæ having disappeared; *b*, *c*, muscular fibres in which the striæ have partly disappeared; *d*, *d*, *d*, globules of fat; *e*, *e*, *e*, starch; *g*, molecular granules.

Whether the gastric juice be entirely incapable of acting upon the muscular substance or not, the above-mentioned facts clearly show that muscular tissue usually is not completely digested in the stomach. The action in this organ is to dissolve the intermuscular fibrous tissue and the sarcolemma, or sheath of the muscular fibres, setting the true muscular substance free and breaking it up into small particles. The mass of tissue is thus reduced to the condition of a thin, pultaceous fluid, which passes into the small intestine, where the process of digestion is completed.

The constituents of the blood, albuminoids, corpuscles etc., which may be introduced in small quantity in connection with muscular tissue, probably are completely dissolved in the stomach.

*Action upon Albumen, Fibrin, Caseine and Gelatine.*—The action of the gastric juice upon uncooked white of egg is to disintegrate its structure, separating and finally dissolving the membranous sacs in which the albumen is contained. It also acts upon the albumen itself, forming a new fluid substance, called albumen-peptone, which, unlike albumen, is not coagulated by heat or acids, but is precipitated by alcohol, tannin and many of the metallic salts. The digestion of raw or imperfectly coagulated albumen takes place with considerable rapidity in the stomach; and the digestion of albumen in this form is more rapid than when it has been completely coagulated by heat. It is a matter of common as well as of scientific observation, that eggs when hard-boiled are less easily digested than when they are soft-boiled or uncooked. The products of the digestion of raw or of coagulated albumen, albumen-peptone, are essentially the same. It is probable that the entire process of digestion and absorption of albumen takes place in the stomach; and if any albumen pass out of the pylorus, the quantity is very small.

Fibrin, as distinguished from the so-called fibrin of the muscular tissue, or myosine, is not a very important article of food. The action of the gastric juice upon it is more rapid and complete than upon albumen. The well known action upon fibrin, of water slightly acidulated with hydrochloric acid, has led some physiologists to assume that the acid is the only constituent in the gastric juice necessary to the digestion of this substance; but observations on the comparative action of acidulated water and of artificial or natural gastric juice show that the presence of the organic matter is necessary to the digestion of this as well as of other nitrogenized alimentary substances. The action of water containing a small proportion of acid is to render fibrin soft and transparent, frequently giving to the entire mass a jelly-like consistence. The result of the digestion of fibrin in the gastric juice or in an acidulated fluid to which pepsine has been added, is its complete solution and transformation into a substance which is not affected by heat, acids or by rennet. The substance resulting from the action of gastric juice upon fibrin, called fibrin-peptone, resembles albumen-peptone, but nevertheless has certain distinctive characters.

Liquid caseine is immediately coagulated by the gastric juice, by the action both of the free acid and the organic matter. Once coagulated, caseine is acted upon in the same way as coagulated albumen. The caseine which is taken as an ingredient of cheese is digested in the same way. According to Lehmann, coagulated caseine requires a longer time for its solution in the stomach than most other nitrogenized substances. The caseine of human milk, which coagulates only into a sort of jelly, is more easily digested than caseine from cow's milk (Elässer). The product of the digestion of caseine is a soluble substance, not coagulable by heat or the acids, called caseine-peptone.

Gelatine is rapidly dissolved in the gastric juice, when it loses the characters by which it is ordinarily recognized, and no longer forms a jelly on cooling. This substance is much more rapidly disposed of than the tissues from which it is formed, and the products of its digestion in the gastric juice resemble the substances resulting from the digestion of the albuminoids generally.

*Action on Vegetable Nitrogenized Substances.*—These substances, of which gluten may be taken as the type, undoubtedly are digested chiefly in the stomach. Raw gluten is acted upon very much in the same way as fibrin, and cooked gluten behaves like coagulated albumen. Vegetable articles of food generally contain gluten in greater or less quantity, or substances resembling it, as well as various non-nitrogenized matters, and cellulose. The fact that these articles are not easily attacked in any portion of the alimentary canal, unless they have been well comminuted in the mouth, is shown by the passage of grains of corn, beans etc., in the fæces. When properly prepared by mastication and insalivation, the action of the gastric juice is to disintegrate them, dissolving out the nitrogenized matters, freeing the starch and other matters so that they may be more easily acted upon in the intestines, and leaving the hard, indigestible matters, such as cellulose, to pass away in the fæces. The nitrogenized constituents of bread are probably acted upon in the stomach in the same way and to the same extent as albumen, fibrin and caseine.

*Peptones.*—It has been shown that gastric digestion is not merely a solution of certain alimentary matters, but that these substances undergo very marked changes and lose the properties by which they are generally recognized. That the different products of this transformation resemble each other very closely is also undoubted; but there are certain differences in the chemical composition of the products of digestion of the different constituents of food, as well as differences, which have lately been noted, as regards their behavior with reagents.

The peptones in solution form colorless liquids, having a feeble odor resembling that of meat. They are not coagulable by heat or by most acids, a property which distinguishes them from almost all of the nitrogenized constituents of food. They are coagulated, however, by many of the metallic salts, by chlorine, and by tannin, in slightly acidulated solutions. On evaporating peptones to dryness, the residue consists of a yellowish-white substance, resembling desiccated white of egg. This is soluble in water, when it regains its characteristic properties, but is entirely insoluble in alcohol.

It is evident that the gastric juice, aside from its action in preparing certain articles for digestion by the intestinal fluids, does not simply liquefy certain of the alimentary matters, but changes them in such a way as to render them osmotic and provides against the coagulation which is so readily induced in ordinary nitrogenized bodies. Peptones pass through membranes with great facility.

Another, the most important and the essential change which is exerted by the gastric juice upon the albuminoids, is that by which they are rendered capable of assimilation by the system after their absorption. Pure albumen and gelatine, when injected into the blood, are not assimilable and are rejected by the kidneys; but albumen and gelatine which have been digested in gastric juice are assimilated in the same way as though they had penetrated by the natural process of absorption from the alimentary canal (Bernard and Barreswil). The same is true of caseine and fibrin. These facts, showing that something more is necessary in gastric digestion than mere solution, point to pepsine as the important agent in producing the peculiar modifications so necessary to proper assimilation of nitrogenized alimentary substances. The action of pepsine is essential to the changes which occur in the albuminoid alimentary matters, resulting in the formation of what are known as peptones; and the change into peptones takes place in all nitrogenized substances that are dissolved in the stomach. This may occur even when the albuminoid matters are somewhat advanced in putrefaction; and the gastric juice possesses antiseptic properties, which fact accounts for the frequent innocuousness of animal substances in various stages of decomposition when taken into the stomach.

The change of the albuminoids into peptones in the stomach is not direct. The intermediate processes probably are the following: The albuminoids are first changed by the gastric juice into an acid-albumen or albuminate; this is farther changed into propeptone, or as it is called by Kühne, hemialbumose; and the final action is a change into the true peptones. These intermediate processes have been studied in artificial digestion, and the acid-albumen and propeptone differ, in some of their chemical properties which it is not necessary to describe in detail, from both albumen and peptone. A temperature near that of the body is necessary to the various changes just mentioned.

*Action of the Gastric Juice on Fats, Sugars and Amylaceous Substances.* —Most of the fatty constituents of the food are liquefied at the temperature of the body; and when taken in the form of adipose tissue, the vesicles in which the fatty matters are contained are dissolved, the fat is set free, is melted and floats in the form of drops of oil on the alimentary mass. The action of the stomach, then, seems to be to prepare the fats, chiefly by dissolving the adipose vesicles, for the complete digestion which takes place in the small intestine.

The varieties of sugar of which glucose is the type undergo little if any change in digestion and are probably in greatest part directly absorbed by the mucous membrane of the stomach. This is not the case, however, with the varieties of sugar classed with cane-sugar. It has been shown that cane-sugar injected into the veins of a living animal is not assimilated by the system but is immediately rejected by the kidneys. When, however, it has been changed into glucose by the action of a dilute acid or by digestion in the gastric juice, it no longer behaves as a foreign substance and does not appear in the urine. Experiments have shown that cane-sugar, after being digested for several hours in the gastric juice, is slowly converted into glucose. This action does not depend upon any constituent of the gastric juice except the free acid; and a dilute mixture of hydrochloric acid had an equally marked effect. Experiments in artificial digestion have shown that cane-sugar is transformed into glucose by the gastric juice very slowly, the action of this fluid in no way differing from that of very dilute acids. In the natural process of digestion, this action may take place to a certain extent; but it is not shown to be constant or important.

The action of gastric juice, unmixed with saliva, upon starch is entirely negative, as far as any transformation into sugar is concerned. When the starch is enclosed in vegetable cells, it is set free by the action of the gastric juice upon the nitrogenized parts. Raw starch in the form of granules becomes hydrated in the stomach, on account of the elevated temperature and the acidity of the contents of the organ. This is not the form, however, in which starch is generally taken by the human subject; but when it is so taken, the stomach evidently assists in preparing it for the more complete processes of digestion which are to take place in the small intestine.

Cooked or hydrated starch, the form in which it exists in bread, farinaceous preparations generally and ordinary vegetables, is not affected by the pure gastric juice and passes out at the pylorus unchanged. It must be remembered, however, that the gastric juice does not entirely prevent a continuance of the action of the saliva; and experiments have shown that gastric juice taken from the stomach, when it contains a notable quantity of saliva, has, to a certain extent, the power of transforming starch into sugar.

The changes which vegetable acids and salts, the various inorganic constituents of food and the liquids which are classed as drinks undergo in the stomach are very slight. Most of these substances can hardly be said to be digested; for they are either liquid or in solution in water and are capable of direct absorption and assimilation. With regard to most of the inorganic salts, they either exist in small quantity in the ordinary water taken as drink or are united with organic nitrogenized substances. In the latter case, they become intimately combined with the organic matters resulting from gastric digestion. It has been noted that the various peptones contain the same inorganic salts which existed in the nitrogenized substances from which they were formed.

Some discussion has arisen with regard to the action of the fluids of the stomach upon calcium phosphate and calcium carbonate, salts which are considered nearly if not entirely insoluble. Observations on both natural and artificial digestion have shown that the calcareous constituents of bone are to a certain extent dissolved in the gastric juice. Bones are digested to a considerable extent in the stomach, although the greater part passes through the alimentary canal and is discharged unchanged in the fæces. In the natural process of digestion, the solution of the calcareous constituents of bone is more rapid than in artificial digestion, from the fact that the juice is being continually absorbed and secreted anew by the mucous membrane of the stomach.

*Duration of Gastric Digestion.*—Inasmuch as comparatively few articles, and these belonging exclusively to the class of organic nitrogenized substances, are completely dissolved in the stomach, it is evident that the length of time during which food remains in this organ, or the time occupied in the solution of food by gastric juice out of the body, does not represent the absolute digestibility of different articles. It is, nevertheless, an important question to ascertain, as nearly as possible, the duration of gastric digestion.

There has certainly never been presented so favorable an opportunity for determining the duration of gastric digestion as in the case of St. Martin. From a great number of observations made on digestion in the stomach itself, Beaumont came to the conclusion that "the time ordinarily required for the disposal of a moderate meal of the fibrous parts of meat, with bread, etc., is three to three and a half hours." The observations of F. G. Smith, made upon St. Martin many years later, gave two hours as the longest time that aliments remained in the stomach. In a case of intestinal fistula reported by Busch, it was noted that food began to pass out of the stomach into the intestines fifteen minutes after its ingestion and continued to pass for three or four hours, until the stomach was emptied.

Undoubtedly, the duration of gastric digestion varies in different individuals and is greatly dependent upon the kind and quantity of food taken, conditions of the nervous system, exercise etc. As a mere approximation, the average time that food remains in the stomach after an ordinary meal may be stated to be between two and four hours.

Milk is one of the articles digested in the stomach with greatest ease. Its highly nutritive properties and the variety of its nutritious constituents render it very valuable as an article of diet, particularly when the digestive powers are impaired and when it is important to supply the system with considerable nutriment. Eggs are likewise highly nutritious and are easily digested. Raw and soft-boiled eggs are more easily digested than hard-boiled eggs. "Whipped" eggs are apparently disposed of with great facility. As a rule the flesh of fish is more easily digested than that of the warm-blooded animals. Oysters, especially when raw, are quite easy of digestion. The flesh of mammals seems to be more easily digested than the flesh of birds. Of the different kinds of meat, venison, lamb, beef and mutton are easily digested, while veal and fat roast-pork are digested with difficulty. Soups are generally very easily digested. The animal substances which are digested most rapidly, however, are tripe, pigs' feet and brains. Vegetable articles are digested in about the same time as ordinary animal food; but a great part of the digestion of these substances takes place in the small intestine. Bread is digested in about the time required for the digestion of the ordinary meats (Beaumont).

*Conditions which influence Gastric Digestion.*—The various conditions which influence gastric digestion, except those which relate exclusively to the character or the quantity of food, operate mainly by influencing the quantity and quality of the gastric juice. It is seldom that temperature has any influence, for the temperature of the stomach in health does not present variations sufficient to have any marked effect upon digestion.

As a rule, gentle exercise, with repose or agreeable and tranquil occupation of the mind, is more favorable to digestion than absolute rest. Violent exercise or severe mental or physical exertion is always undesirable immediately after the ingestion of a large quantity of food, and as a matter of common experience, has been found to retard digestion.

The effects of sudden and considerable loss of blood upon gastric digestion are very marked. After a full meal, the whole alimentary tract is deeply congested, and this condition is undoubtedly necessary to the secretion, in proper quantity, of the various digestive fluids. When the entire quantity of blood in the economy is greatly diminished from any cause, there is difficulty in supplying the amount of gastric juice necessary for a full meal, and disorders of digestion are likely to occur, especially if a large quantity of food have been taken. This is also true in inanition, when the quantity of blood is greatly diminished. In this condition, although the system constantly craves nourishment and the appetite frequently is enormous, food should be taken in small quantities at a time.

As a rule children and young persons digest food which is adapted to them more easily and in larger relative quantity than those in adult life or in old age; but ordinarily in old age digestion is carried on with more vigor and regularity than the other vegetative processes, such as general assimilation, circulation and respiration.

*Influence of the Nervous System on the Stomach.*—It is well known that mental emotions frequently have a marked influence on digestion, and this, of course, can take place only through the nervous system. Of the two nerves which are distributed to the stomach, the pneumogastric has been the more carefully studied, experiments upon the sympathetic being more difficult. Although the complete history of the influence of the pneumogastrics upon digestion belongs to the physiology of the nervous system, it will be useful in this connection to consider briefly some of the facts which have been ascertained with regard to the influence which these nerves exert upon the stomach.

The experiments of Bernard and others have shown that the vascular mechanism of the mucous membrane is to a great extent under the influence of the pneumogastrics. If these nerves be divided while gastric digestion is at its height, the mucous membrane immediately becomes pale, and the secretion of gastric juice is nearly if not quite arrested. It has been found, however, that gastric juice may be secreted in small quantity under the stimulus of food, even when both pneumogastrics and the sympathetic nerves going to the stomach have been divided (Heidenhain).

Section of both pneumogastrics, while it does not entirely paralyze the muscular coat of the stomach, renders its contractions irregular and feeble. It is stated that section of these nerves is followed by "a short temporary contraction of the cardiac aperture" (Stirling).

*Movements of the Stomach.*—As the articles of food are passed into the stomach by the acts of deglutition, the organ gradually changes its form, size and position. When the stomach is empty, the opposite surfaces of its lining membrane are in contact in many parts and are thrown into longitudinal folds. As the organ is distended, these folds are effaced, the stomach itself becoming more rounded, and as the two ends, with the lesser curvature are comparatively immovable, the whole organ undergoes a movement of rotation, by which the anterior face becomes superior and is applied to the diaphragm. At this time the great pouch has nearly filled the left hypochondriac region; the greater curvature presents anteriorly and comes in contact with the abdominal walls. Aside from these changes, which are merely due to the distention, the stomach undergoes important movements, which continue until its contents have been dissolved and absorbed or have passed out at the pylorus; but while these movements are taking place, the two orifices are guarded, so that the food shall remain for the proper time exposed to the action of the gastric juice. By the rhythmical contractions of the lower extremity of the œsophagus, regurgitation of food is prevented; and the circular fibres, which form a thick ring at the pylorus, are constantly contracted, so that—at least during the first periods of digestion—only liquids and that portion of food which has been reduced to a pultaceous consistence can pass into the small intestine. It is well known that this resistance at the pylorus does not endure indefinitely, for indigestible articles of considerable size, such as stones, have been passed by the anus after having been introduced into the stomach; but observations have shown that masses of digestible matter are passed by the movements of the stomach to the pylorus, over and over again, and that they do not find their way into the intestine until they have become softened and more or less disintegrated.

The contractions of the walls of the stomach are of the kind characteristic of the non-striated muscular fibres. If the finger be introduced into the stomach of a living animal during digestion, it is gently but rather firmly grasped by a contraction, which is slow and gradual, enduring for a few seconds and as slowly and gradually relaxing and extending to another part of the organ. The movements during digestion present certain differences in different animals; but there can be no doubt that the phenomenon is universal. In dogs, when the abdomen is opened soon after the ingestion of food, the stomach appears pretty firmly contracted on its contents. In a case reported by Todd and Bowman, in the human subject, in which the stomach was very much hypertrophied and the walls of the abdomen were very thin, the vermicular movements could be distinctly seen. These movements were active, resembling the peristaltic movements of the intestines, for which, indeed, they were mistaken, as the nature of the case was not recognized during life. No argument, therefore, seems necessary to show that during digestion, the stomach is the seat of tolerably active movements.

A peculiarity in the movements of the stomach, which has been repeatedly observed in the lower animals, particularly dogs and cats, and in certain cases has been confirmed in the human subject, is that at about the junction of the cardiac two-thirds with the pyloric third, there is frequently a transverse band of fibres so firmly contracted as to divide the cavity into two almost distinct compartments. It has also been noted that the contractions in the cardiac division are much less vigorous than near the pylorus; the stomach seeming simply to adapt itself to the food by a gentle pressure as it remains in the great pouch, while in the pyloric portion, divided off as it is by the hour-glass contraction above mentioned, the movements are more frequent, vigorous and expulsive.

As the result chiefly of the observations of Beaumont, the following may be stated as a summary of the physiological movements of the stomach in digestion:

The stomach normally undergoes no movements until food is passed into its cavity. When food is received, at the same time that the mucous membrane becomes congested and the secretion of gastric juice begins, contractions of the muscular coat occur, which are at first slow and irregular, but become more vigorous and regular as the process of digestion advances. After digestion has become fully established, the stomach is generally divided, by the firm and almost constant contraction of an oblique band of fibres, into a cardiac and a pyloric portion; the former occupying about two-thirds, and the latter, one-third of the length of the organ. The contractions of the cardiac division of the stomach are uniform and rather gentle; while in the pyloric division, they are intermittent and more expulsive. The effect of the contractions of the stomach upon the food contained in its cavity is to subject it to a tolerably uniform pressure in the cardiac portion, the general tendency of the movement being toward the pylorus, along the greater curvature, and back from the pylorus toward the great pouch, along the lesser curvature. At the constricted part which separates the cardiac from the pyloric portion, there is an obstruction to the passage of the food until it has been sufficiently acted upon by the secretions in the cardiac division to have become reduced to a pultaceous consistence. The alimentary mass then passes into the pyloric division, and by a more powerful contraction than occurs in other parts of the stomach, it is passed into the small intestine.

The revolutions of the alimentary mass, thus accomplished, take place slowly, by gentle and persistent contractions of the muscular coat; the food occupying two or three minutes in its passage entirely around the stomach. Every time that a revolution is accomplished, the contents of the stomach are somewhat diminished in quantity; probably, in a slight degree, from absorption of digested matter by the stomach itself, but chiefly by the gradual passage of the softened and disintegrated mass into the small intestine. This process continues until the stomach is emptied, lasting between two and four hours; after which, the movements of the stomach cease until food is again introduced.

Regurgitation of food by contractions of the muscular coats of the stomach, eructation, or the expulsion of gas, and vomiting are not physiological acts. It has been shown that vomiting is produced by contractions of the abdominal muscles and the diaphragm, compressing the stomach, which is passive, except that the pyloric opening is firmly closed, the cardiac opening being relaxed. Eructation, although usually involuntary, is sometimes under the control of the will. When it occurs, while it is difficult or impossible to prevent the discharge of the gas, the accompanying sound may be readily suppressed. Eructation frequently becomes a habit, which in many persons is so developed by practice that the act may be performed voluntarily at any time. The gaseous contents of the stomach during digestion are composed of oxygen, carbon dioxide, hydrogen and nitrogen, in proportions that are very variable.

# CHAPTER IX.

## *INTESTINAL DIGESTION.*

**Physiological anatomy of the small intestine—Glands of Brunner—Intestinal tubules, or follicles of Lieberkühn—Intestinal villi—Solitary glands, or follicles, and patches of Peyer—Intestinal juice—Action of the intestinal juice in digestion—Pancreatic juice—Action of the pancreatic juice upon starches and sugars—Action upon nitrogenized substances—Action upon fats—Action of the bile in digestion—Biliary fistula—Variations in the flow of bile—Movements of the small intestine—Peristaltic and antiperistaltic movements—Uses of the gases in the small intestine—Physiological anatomy of the large intestine—Processes of fermentation in the intestinal canal—Contents of the large intestine—Composition of the fæces—Excretine and excretoleic acid—Stercorine—Indol, skatol, phenol etc.—Movements of the large intestine—Defæcation—Gases found in the alimentary canal.**

### PHYSIOLOGICAL ANATOMY OF THE SMALL INTESTINE.

THE small intestine, extending from the pyloric extremity of the stomach to the ileo-cæcal valve, is loosely held to the spinal column by a double fold of serous membrane, called the mesentery. As the peritoneum which lines the cavity of the abdomen passes from either side to the spinal column, it comes together in a double fold just in front of the great vessels along the spine, and passing forward, it divides again into two layers, which become continuous with each other and enclose the intestine, forming its external coat. The width of the mesentery is usually three to four inches (7·62 to 10·16 centimetres); but at the beginning and at the termination of the small intestine, it suddenly becomes shorter, binding the duodenum and that portion of the intestine which opens into the caput coli closely to the subjacent parts. The mesentery thus keeps the intestine in place, but it allows a certain degree of motion, so that the tube may become convoluted, accommodating itself to the size and form of the abdominal cavity. The form of these convolutions is irregular and is continually changing. The length of the small intestine, according to Gray, is about twenty feet (6·1 metres); but the canal is very distensible, and its dimensions are subject to frequent variations. Its average diameter is about an inch and a quarter (3·18 centimetres).

The small intestine has been divided into three portions, which present anatomical and physiological peculiarities, more or less marked. These are the duodenum, the jejunum and the ileum.

The duodenum has received its name from the fact that it is about the length of the breadth of twelve fingers, or eight to ten inches (20·32 to 25·4 centimetres). This portion of the intestine is considerably wider than the constricted pyloric end of the stomach, with which it is continuous, and is also much wider than the jejunum.

The coats of the duodenum, like those of the other divisions of the intestinal tube, are three in number. The external is the serous, or peritoneal coat, which has already been described. The middle, or muscular coat is composed of non-striated muscular fibres, such as exist in the stomach, arranged in two layers. The external, longitudinal layer is not very thick, and the direction of its fibres can be made out easily only at the outer portions of the tube, opposite the attachment of the mesentery. Near the mesenteric border the outlines of the fibres are very faint. This is true throughout the whole of the small intestine; although the fibres are most abundant in the duodenum. The internal layer of fibres is considerably thicker than the longitudinal layer. These fibres encircle the tube, running generally at right angles to the external layer, but some of them having rather an oblique direction. The circular layer is thickest in the duodenum, diminishing gradually in thickness to the middle of the jejunum, but afterward maintaining a nearly uniform thickness throughout the canal, to the ileo-cæcal valve.

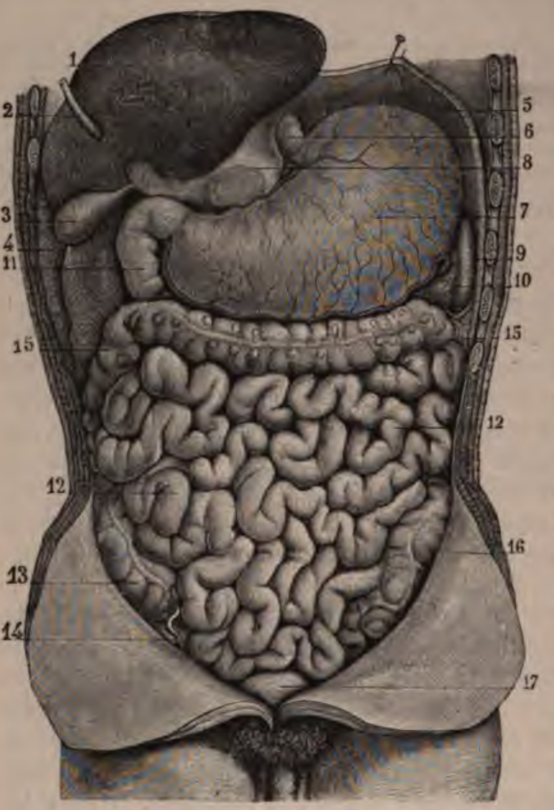


FIG. 66.—*Stomach, liver, small intestine etc.* (Sappey).
1, *inferior surface of the liver*; 2, *round ligament of the liver*; 3, *gall-bladder*; 4, *superior surface of the right lobe of the liver*; 5, diaphragm; 6, lower portion of the œsophagus; 7, *stomach*; 8, *gastro-hepatic omentum*; 9, spleen; 10, *gastro-splenic omentum*; 11, *duodenum*; 12, 12, *small intestine*; 13, *cæcum*; 14, *appendix vermiformis*; 15, 15, *transverse colon*; 16, *sigmoid flexure of the colon*; 17, urinary bladder.

The jejunum, the second division of the small intestine, is continuous with the duodenum. It presents no well marked line of separation from the third division, but is generally considered as including the upper two-fifths of the small intestine, the lower three-fifths being called the ileum. It has received the name jejunum from the fact that it is almost always found empty after death.

The ileum is somewhat narrower and thinner than the jejunum, otherwise possessing no marked peculiarities except in its mucous membrane. This division of the intestine opens into the colon.

*Mucous Membrane of the Small Intestine.*—The mucous coat of the small intestine is somewhat thinner than the lining membrane of the stomach. It is thickest in the duodenum and gradually becomes thinner toward the ileum. It is highly vascular, presenting, like the mucous membrane of the stomach, a great increase in the quantity of blood during digestion. It has a peculiar soft and velvety appearance, and during digestion it is of a vivid-red color, being pale pink during the intervals. It presents for anatomical description the following parts: 1, folds of the membrane, called valvulæ conniventes; 2, duodenal racemose glands, or glands of Brunner; 3, intestinal tubules, or follicles of Lieberkühn; 4, intestinal villi; 5, solitary glands, or follicles; 6, agminated glands, or patches of Peyer.

The valvulæ conniventes, simple transverse duplicatures of the mucous membrane of the intestine, are particularly well marked in man, although they are found in some of the inferior animals belonging to the class of mammals, as the elephant and the camel. They render the extent of the mucous membrane much greater than that of the other coats of the intestine. Beginning at about the middle of the duodenum, they extend, with no diminution in number, throughout the jejunum. In the ileum they progressively diminish in number, until they are lost at about its lower third. There are about six hundred of these folds in the first half of the small intestine and two hundred to two hundred and fifty in the lower half (Sappey). In those portions of intestine where they are most abundant, they increase the length of the mucous membrane to about double that of the tube itself; but in the ileum they do not increase the length more than one-sixth. The folds are always transverse and occupy usually one-third to one-half of the circumference of the tube, although a few may extend entirely around it. The greatest width of each fold is at its centre, where it measures a quarter to half an inch (6·4 to 12·7 mm.). From this point the width gradually diminishes until the folds are lost in the membrane as it is attached to the muscular coat. Between the folds are found fibres of connective tissue similar to those which attach the membrane throughout the whole of the alimentary tract. This, though loose, is constant, and it prevents the folds from being effaced, even when the intestine is distended to its utmost. Between the folds are also found blood-vessels, nerves and lymphatics.

The position and arrangement of the valvulæ conniventes are such that they move freely in both directions and may be applied to the inner surface of the intestine either above or below their lines of attachment. It is evident that the food, as it passes along in obedience to the peristaltic movements, must, by insinuating itself beneath the folds and passing over them, be exposed to a greater extent of mucous membrane than if these valves did not exist. This is about the only definite use that can be assigned to them.

FIG. 67.—*Gland of Brunner, from the human subject (Frey).*

Thickly set beneath the mucous membrane in the first half of the duodenum, and scattered here and there throughout the rest of its extent, are the duodenal racemose glands, or the glands of Brunner. These are not found in other parts of the intestinal canal. In their structure they closely resemble the racemose glands of the œsophagus. On dissecting the muscular coat from the mucous membrane, they may be seen with the naked eye, in the areolar tissue, in the form of little, rounded bodies, about one-tenth of an inch (2·5 mm.) in diameter. Examined microscopically, these bodies are found to consist of a large number of rounded follicles held together by a few fibres of connective tissue. They have blood-vessels ramifying on their exterior and are lined with glandular epithelium. They communicate with an excretory duct which penetrates the mucous membrane and opens into the intestinal cavity When these structures are examined in a perfectly fresh preparation, the excretory duct is frequently found to contain a clear, viscid mucus, of an alkaline reaction. This secretion has never been obtained in quantity sufficient to admit of the determination of its chemical or physiological properties. Its quantity must be very small, compared with the secretion produced by the follicles of Lieberkühn.

The intestinal tubules, or follicles of Lieberkühn, the most important glandular structures in the intestinal mucous membrane, are found through-

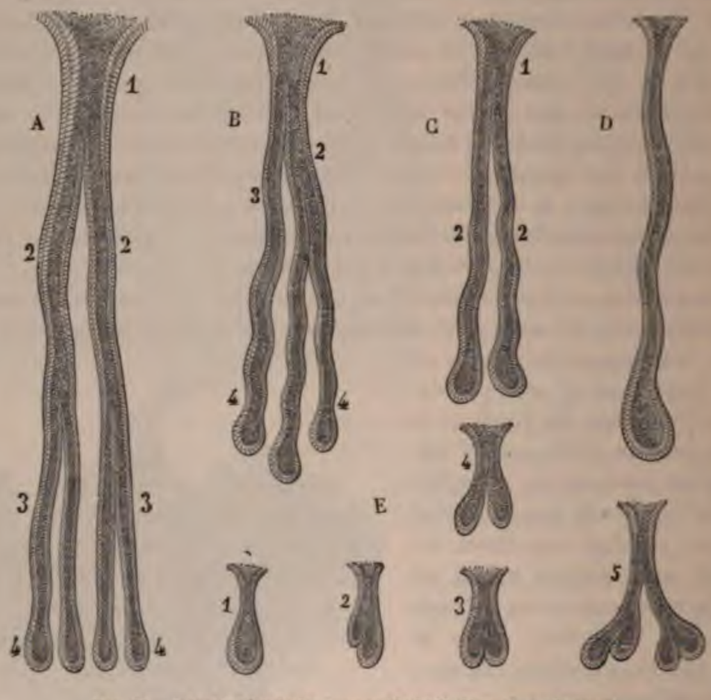


FIG. 68.—*Intestinal tubules; magnified* 100 *diameters* (Sappey).

A. From the dog. 1, excretory canal; 2, 2, primary branches; 3, 3, secondary branches; 4, 4, terminal *culs-de-sac.*
B. From the ox. 1, excretory canal; 2, principal branch dividing into two; 3, branch undivided; 4, 4, terminal *culs-de-sac.*
C. From the sheep. 1, trunk; 2, 2, branches.
D. Single tube, from the pig.
E. From the rabbit and hare. 1, simple gland; 2, 3, 4, bifid glands; 5, compound gland from the duodenum.

out the whole of the small and large intestines. In examining a thin section of the mucous membrane, these little tubes are seen closely packed together, occupying nearly the whole of its structure. Between the tubules, are blood-vessels, embedded in a dense stroma of fibrous tissue with non-striated muscular fibres. In vertical sections of the mucous membrane, the only situations where the tubules are not seen are in that portion of the duodenum occupied by the ducts of the glands of Brunner and immediately over the centre of the larger solitary glands and some of the closed follicles which are collected to form the patches of Peyer. The tubes are not entirely absent in the patches of Peyer, but are here collected in rings, twenty or thirty tubes deep, which surround each of the closed follicles. Microscopical examination of the surface of the mucous membrane by reflected light shows that the openings of the tubules are between the villi.

The tubules usually are simple, though sometimes bifurcated, are composed externally of a structureless basement-membrane, and are lined with a layer of cylindrical epithelium like the cells which cover the villi, the only difference being that in the tubes the cells are shorter. These cells never contain fatty granules, even during the digestion of fat. The central cavity which the cells enclose, which is about one-fourth of the diameter of the tube, is filled with a clear, viscid fluid, which is the most important constituent of the intestinal juice. The length of the tubules is equal to the thickness of the muccus membrane and is about $\frac{1}{75}$ of an inch (0·33 mm.). Their diameter is about $\frac{1}{360}$ of an inch (0·07 mm.). In man they are cylindrical, terminating in a single, rounded, blind extremity, which frequently is a little larger than the rest of the tube. These tubules are the chief agents concerned in the production of the fluid known as the intestinal juice.

The intestinal villi, though chiefly concerned in absorption, are most conveniently considered in this connection. These exist throughout the whole of the small intestine, but are not found beyond the ileo-cæcal valve, although they cover that portion of the valve which looks toward the ileum. Their number is very great, and they give to the membrane its peculiar and characteristic velvety appearance. They are found on the valvulæ conniventes as well as on the general surface of the mucous membrane. They are most abundant in the duodenum and jejunum. Sappey estimated, as an average, about 6,450 to the square inch (1,000 in a square centimetre) and more than ten millions (10,125,000) throughout the whole of the small intestine. In the human subject the villi are flattened cylinders or cones. In the duodenum, where they resemble somewhat the elevations found in the pyloric portion of the stomach, they are shorter and broader than in other situations and are more like flattened, conical folds. In the jejunum and ileum they are in the form of long, flattened cones and cylinders. As a rule the cylindrical form predominates in the lower portion of the intestine. In the jejunum they attain their greatest length, measuring here $\frac{1}{30}$ to $\frac{1}{20}$ of an inch (0·83 to 1·25 mm.) in length by $\frac{1}{70}$ to $\frac{1}{120}$ of an inch (0·36 to 0·21 mm.) in breadth at their base.

The structure of the villi shows them to be simple elevations of the mucous membrane, provided with blood-vessels and with lacteals, or intestinal lymphatics. Externally is found a single layer of long, cylindrical epithelial cells, resting on a structureless basement-membrane. These cells, though closely adherent to the subjacent parts during life, are easily detached after death and are almost always destroyed and removed in injected preparations. They adhere firmly to each other and are isolated with difficulty in microscopical preparations. The borders of the free surfaces of these cells are thickened and finely striated, forming, as it were, a special membrane covering the villus and external to the cells. Between the cylindrical cells are a few of the so-called goblet-cells similar to those found on the mucous membrane of the stomach (see Fig. 60, page 214).


FIG. 69.—*Intestinal villus* (Leydig).

*a, a, a*, epithelial covering; *b, b*, capillary net-work; *c, c*, longitudinal muscular fibres; *d*, lacteal.

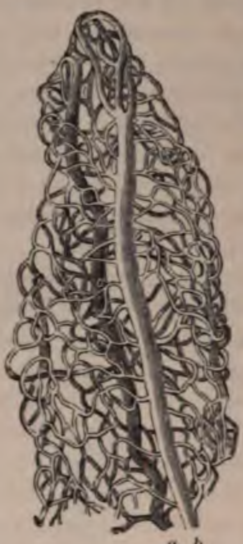


FIG. 70.—*Capillary net-work of an intestinal villus* (Frey).

*a*, venous trunk; *b*, arterial trunk.

The substance of the villus is composed of amorphous matter, in which are embedded nuclei and a few fibres, fibro-plastic cells and non-striated muscular fibres. The blood-vessels are very abundant; four or five, and sometimes as many as twelve or fifteen arterioles entering at the base, ramifying through the substance of the villus, but not branching or anastomosing or even diminishing in caliber until, by a slightly wavy turn or loop, they communicate with the venous radicles, each of which is somewhat larger than the arterioles. The veins all converge to two or three branches, finally emptying into a large trunk situated nearly in the long axis of the villus.

The muscular fibres of the villi are longitudinal, forming a thin layer surrounding the villus, about half-way between the periphery and the centre, and continuous with the muscular coat of the intestine.

FIG. 71.—*Epithelium of the small intestine of the rabbit* (Funke).

In the central portion of each villus, is a small lacteal, one of the vessels of origin of the lacteal system, with an extremely delicate wall composed of endothelial cells with frequent stomata, or small openings, between their borders. This vessel is probably in the form of a single tube, either simple or presenting a few short, rounded diverticula.

The stomata of the lacteal vessel are thought to communicate with lymph-spaces or canals in the substance of the villus. Owing to the excessive tenuity of the walls of the lacteals in the villi, it has been found impossible to fill these vessels with an artificial injection, although the lymphatics subjacent to them may be easily distended and studied in this way.

No satisfactory account has ever been given of nerves in the intestinal villi. If any exist in these structures, they probably are derived from the sympathetic system.

The solitary glands, or follicles, and the patches of Peyer, or agminated glands, have one and the same structure, the only difference being that those called solitary are scattered singly in very variable numbers throughout the small and large intestine, while the agminated glands consist of these follicles collected into patches of different sizes. These patches are generally found in the ileum. The number of the solitary glands is very variable, and they are sometimes absent. The patches of Peyer are always situated in that portion of the intestine opposite the attachment of the mesentery. They are likewise variable in number and are irregular in size. They usually are irregularly oval in form, and measure half an inch to an inch and a half (12·7 to 38·1 mm.), in length by three-fourths of an inch (19·1 mm.) in breadth. Sometimes they are three to four inches (7·6 to 10·1 centimetres) long, but the largest are always found in the lower part of the ileum. Their number is about twenty, and they are generally confined to the ileum; but when they are very abundant—for they sometimes exist to the number of sixty or eighty—they may be found in the jejunum or even in the duodenum.

Two varieties of the patches of Peyer have been described by anatomists. In one of these varieties, the patch is quite prominent, its surface being slightly raised above the general mucous surface; in the other, the surface is smooth, and the patch is distinguished at first with some difficulty. The more prominent patches are covered with mucous membrane arranged in folds something like the convolutions on the surface of the brain. The valvulæ conniventes cease at or very near their borders. These are the only patches which are generally described as the glands of Peyer, the others, which may be called the smooth patches, being frequently overlooked. The latter are covered with a smooth, thin, and closely adherent mucous membrane. Their follicles are small and abundant. The borders of these patches are much less strongly marked than in those of the first variety. As they are evident only upon close examination and as they are the only patches present in certain individuals, it is said that sometimes the patches of Peyer are wanting. They are usually in less number than the first variety.

The villi are very large and prominent on the mucous membrane covering the first variety of Peyer's patches, especially at the summit of the folds. In the second variety the villi are the same as over other parts of the mucous membrane, except that they are placed more irregularly and are not so abundant.

The follicles which form the patches of Peyer are completely closed and are somewhat pear-shaped, with their pointed projections directed toward the cavity of the intestine. Just above the follicle, there generally is a small opening in the mucous membrane, surrounded by a ring of intestinal tubules, and leading to a cavity, the base of which is convex and is formed by the conical projection of the follicle. The diameter of the follicles is $\frac{1}{75}$ to $\frac{1}{25}$ or $\frac{1}{12}$ of an inch (0·34 to 1 or 2 mm.) The small follicles generally are covered by mucous membrane and have no opening leading to them. Each follicle consists of a rather strong capsule composed of an almost homogeneous or slightly fibrous membrane, enclosing a semi-fluid, grayish substance, cells, blood-vessels and possibly lymphatics. The semi-fluid matter is of an albuminoid character. The cells are very small, rounded, and mingled with small, free nuclei. The blood-vessels have rather a peculiar arrangement. In the first place they are distributed between the follicles, so as to form a rich net-work surrounding each one. Capillary branches are sent from these vessels into the interior of the follicle, returning in the form of loops. Lymphatic vessels have not been distinctly shown within the investing membrane. They have been demonstrated surrounding the follicles, but it is still doubtful whether they exist in their interior. All that is known is that during digestion, the number of lacteals coming from the Peyerian patches is greater than in other parts of the mucous membrane; but vessels containing a milky fluid are never seen within the follicles.

FIG. 72.—*Patch of Peyer* (Sappey).
1, 1, 1, patch of Peyer; 2, 2, folds seen on the surface; 3, 3, grooves between the folds; 4, 4, *fossettes* between some of the folds; 5, 5, 5, 5, 5, 5, 5, 5, valvulæ conniventes; 6, 6, 6, 6, solitary glands; 7, 7, 7, 7, smaller solitary glands; 8, 8, solitary glands upon the valvulæ conniventes.

The description of the follicles which compose the patches of Peyer answers, in general terms, for the solitary glands, except that the latter are found in both the small and large intestines.

## INTESTINAL JUICE.

Of the three fluids with which the food is brought in contact in the intestinal canal, namely, the bile, the pancreatic juice and the intestinal juice, the last, the secretion of the mucous membrane of the small intestine, pre-

FIG. 73.—*Patch of Peyer, seen from its attached surface* (Sappey).
1, 1, serous coat of the intestine; 2, 2, 2, 2, serous coat removed to show the patch; 3, 3, fibrous coat of the intestine; 4, 4, patch; 5, 5, 5, 5, 5, 5, 5, 5, valvulæ conniventes.

sents the greatest difficulties in the investigation of its properties and uses. If it be admissible to reason from the known mechanism of secretion in other parts, it is fair to suppose that the normal secretion of the glands in the mucous membrane of the small intestine can take place only under the stimulus of food. The same cause excites the secretion of the pancreatic juice and increases the flow of bile; and the food, as it passes from the stomach into the duodenum, is to a great extent disintegrated and is mingled with the secretions from both the mouth and the stomach. Under these circumstances, it is evidently impossible to collect the intestinal juice under perfectly physiological conditions, in a state of purity sufficient to admit of extended experiments regarding its composition, properties, and action in digestion.

The experiments of Bidder and Schmidt, Thiry, Colin, Meade Smith and others have given but little positive information with regard to the general properties, even, of the intestinal juice, to say nothing of its digestive action. It may be stated in general terms, that the physiologists just mentioned have attempted to obtain the pure secretion of the follicles of Lieberkühn by isolating portions of the intestine and either taking the secretion as it formed spontaneously or exciting the action of the glands by various means. When it is remembered how different the secretion of the stomach, under the natural stimulus of food, is from the fluid produced during the intervals of digestion, it is evident that little reliance is to be placed upon the experiments that have thus far been made upon the lower animals. Nearly all observers agree, however, that the intestinal juice which they have been able to collect is yellow, thin and strongly alkaline. Some have found it thin and opalescent, while others state that it is viscid and clear. According to Colin the closed follicles of the intestine produce a viscid fluid, which probably exudes through their walls. Colin came to this conclusion from observations upon a large, ribbon-shaped agminate gland, about six feet (183 centimetres) in length, which exists in the small intestine of the pig. In a case of fistula into the upper third of the intestine in the human subject, produced by a penetrating wound of the abdomen—which will be referred to again—Busch found a fluid that was white or of a pale rose-color, rather viscid and always strongly alkaline. The maximum proportion of solid matter which it contained was 7·4 and the minimum, 3.87 per cent. The secretion apparently could not be obtained in sufficient quantity for ultimate analysis. No better opportunity than this has been presented for studying the intestinal juice in its pure state. The nature of the case made it impossible that there should be any admixture of food, pancreatic juice, bile or the secretion of the duodenal glands; and during the process of digestion, the lower part of the intestine undoubtedly produced a perfectly normal fluid.

From what has been ascertained by experiments upon the lower animals and observations on the human subject, the intestinal juice has been shown to possess the following characters:

Its quantity in any portion of the mucous membrane which can be examined is small; but when the extent of the canal is considered, it is evident that the entire quantity of intestinal juice must be great, although beyond this, no reliable estimate can be made.

The intestinal juice is viscid and has a tendency to adhere to the mucous membrane. It generally is either colorless or of a faint rose-tint, and its reaction is invariably alkaline.

With regard to the composition of the intestinal juice, little of a definite character has been learned. All that can be said is that its solid constituents exist in the proportion of about five and a half parts per hundred. In most analyses of fluids from the intestine, there is reason to believe that the normal intestinal juice was not obtained.

The structures which secrete the fluid known as the intestinal juice are the follicles of Lieberkühn, the glands of Brunner and possibly the solitary follicles and patches of Peyer. The secretion, however, is produced chiefly by the follicles of Lieberkühn. Although the other structures mentioned do not contribute much to the secretion, they produce a certain quanity of fluid; and the intestinal juice must be regarded as a compound fluid, like the saliva, and not as the product of a single glandular organ, like the pancreatic juice.

*Action of the Intestinal Juice in Digestion.*—The physiological action of the intestinal juice has been studied in the inferior animals by Frerichs, Bidder and Schmidt and many others; but their experiments have been somewhat contradictory. All are agreed, however, that this fluid is more or less active in transforming starch into sugar. The observations of Busch, on the case of intestinal fistula in the human subject, have given the most satisfactory and definite information on this point. In many regards these observations simply confirm those which have been made upon the inferior animals, but they are of great value, as they establish many important facts relating to the physiological action of the intestinal juice in the human subject.

The case reported by Busch was that of a woman, thirty-one years of age, who, in the sixth month of her fourth pregnancy, was injured in the abdomen by being tossed by a bull. The wound was between the umbilicus and the pubes, presenting two contiguous openings connected with the intestinal canal. It was supposed that the openings were into the upper third of the small intestine. At the time the patient first came under observation, every thing that was taken into the stomach was discharged by the upper opening, and all attempts to establish a communication between the two by a surgical operation had failed. At this time the patient was extremely emaciated, had a voracious appetite, and was evidently suffering from defective nutrition resulting from the constant discharge of alimentary matters from the fistula. Having been treated, however, by the introduction of cooked food into the opening connected with the lower end of the intestine, she soon improved in her nutrition and was then made the subject of extended observations upon intestinal digestion.

In this case, starch, both raw and hydrated, when introduced into the lower opening, where it came in contact only with the intestinal juice, was invariably changed into glucose. Cane-sugar was not transformed into glucose but appeared in the fæces as cane-sugar; and this is important with reference both to the want of action of the intestinal juice upon cane-sugar and the fact that cane-sugar, as such, is not absorbed in quantity by the intestinal mucous membrane.

Coagulated albumen and cooked meats were always more or less digested by the intestinal juice. This fact coincides with the observations of Bidder and Schmidt in their experiments upon dogs and cats.

The observations which were made on fats, melted butter and cod-liver oil showed that the pure intestinal juice had little or no action upon them. These substances always appeared in the fæces unchanged. When, however, fatter matters were taken into the stomach, they were discharged from the upper opening in the intestine, in the form of a very fine emulsion, and could not be recognized as fat.

It is evident from these facts, that the intestinal juice is important in digestion, more as a fluid which aids the general process as it takes place in the small intestine than as one having a peculiar action upon any distinct class or classes of alimentary substances. It undoubtedly assists in completing the digestion of the albuminoids and in transforming starch into sugar. Although, in the latter process, its action is very marked, the same property belongs to the saliva and the pancreatic juice. Intimately mingled—as it always is during digestion—with the bile and the pancreatic juice as well as with various alimentary substances, the intestinal juice should be studied as it acts upon the food in connection with the other fluids found in the small intestine.

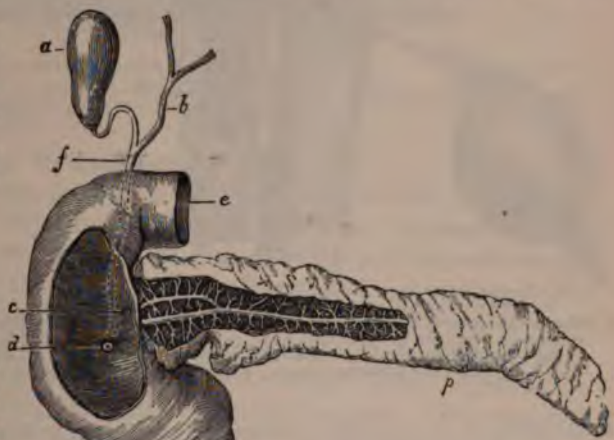


FIG. 74.—*Gall-bladder, ductus choledochus and pancreas* (Le Bon). *a*, gall-bladder; *b*, hepatic duct; *c*, opening of the second duct of the pancreas; *d*, opening of the main pancreatic duct and the bile-duct; *e*, *e*, duodenum; *f*, ductus choledochus; *p*, pancreas.

### Pancreatic Juice.

The pancreas is situated transversely in the upper part of the abdominal cavity and is closely applied to its posterior wall. Its form is elongated, presenting an enlarged, thick portion, called the head, which is attached to the duodenum, a body, and a pointed extremity, which latter is in close relation to the hilum of the spleen. Its average weight is four to five ounces (114·4 to 141·7 grammes); its length is about seven inches (17·78 centimetres); its greatest breadth, about an inch and a half (3·81 centimetres); and its thickness, three-quarters of an inch (1·91 centimetre). It lies behind the peritoneum, which covers only its anterior surface.

There are nearly always, in the human subject, two pancreatic ducts opening into the duodenum; one which opens in common with the ductus communis choledochus, and one which opens about an inch (25·4 mm.) above the main duct. The main duct is about an eighth of an inch (3·2 mm.) in diameter and extends along the body of the gland, becoming larger as it approaches the opening. The second duct is smaller and becomes diminished in caliber as it passes to the duodenum. In general appearance and in minute structure, the pancreas resembles the parotid and submaxillary glands.

The normal pancreatic juice may be obtained by establishing a temporary fistula in the main pancreatic duct of a living animal (Bernard). This may be done in the dog, the pancreas being exposed by an incision in the right hypochondrium, and a canula of proper size being introduced through a slit made in the duct, and secured by a ligature. The external wound is then closed and the end of the tube is allowed to project from the abdomen. The fluid as it is discharged from the tube may be collected in a test-tube, or a thin gum-elastic bag, may be attached.

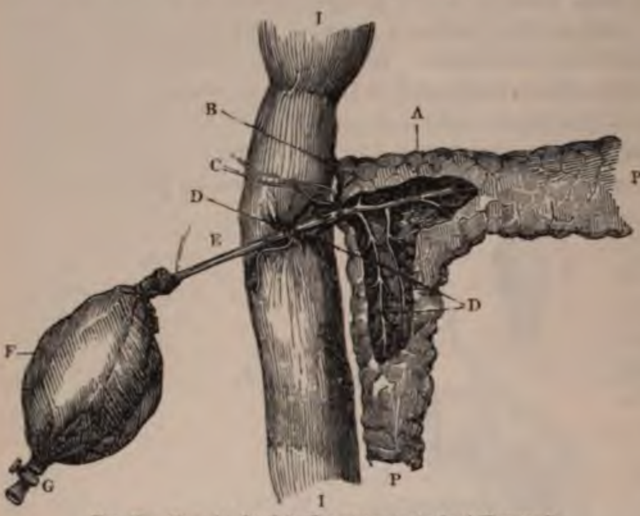


FIG. 75.—*Canula fixed in the pancreatic duct* (Bernard).

A, principal pancreatic duct of the dog; B, smaller pancreatic duct; C, ligature securing a canula in the principal duct; D, D, ligature attaching the canula to the intestine, for security; E, canula; F, bladder, provided with a stop-cock G, to collect the pancreatic juice; P, P, pancreas; I, I, intestine.

Like the other digestive fluids, the pancreatic juice is secreted in abundance only during digestion. It is therefore necessary to feed the animal moderately about an hour before the operation, so that the pancreas may be in full activity. When the gland is exposed at that time, it is filled with blood and has a rosy tint, contrasting strongly with its pale appearance during the intervals of digestion.

The secretion of normal pancreatic juice is entirely suspended during the intervals of digestion. This fact can be observed by opening animals in digestion and while fasting. During digestion the pancreatic duct is always found full of normal secretion; and during the intervals it generally is empty. The secretion begins to flow into the duodenum during the first periods of gastric digestion, before alimentary matters have begun to pass in quantity into the intestine (Bernard). The secretion is readily modified by irritation and inflammation following the operation of making the fistula. The normal pancreatic juice is strongly alkaline, viscid and coagulable by


FIG. 76.—*Pancreatic fistula* (Bernard).

Full-grown shepherd-dog (female), in which a pancreatic fistula has been established. A, silver tube to which a bladder has been attached; B, bladder; C, stop-cock for the purpose of collecting the juice which accumulates in the bladder.

heat. It is almost always the case that a few hours after the canula is fixed in the duct, the juice loses some of these characters and flows in abnormal quantity. With respect to susceptibility to irritation, the pancreas is peculiar; and its secretion is sometimes abnormal from the first moments of the experiment, especially if the operative procedure have been prolonged and difficult. That the properties above described are characteristic of the normal pancreatic secretion, there can be no doubt; as in all instances, fluid taken from the pancreatic duct of an animal suddenly killed while in full digestion is strongly alkaline, viscid and coagulable by heat. This excessive sensitiveness of the pancreas rendered fruitless all the attempts to establish a permanent pancreatic fistula from which the normal juice could be collected (Bernard). The fluid collected from a permanent fistula does not represent the normal secretion.

*General Properties and Composition of the Pancreatic Juice.*—In all the inferior animals from which the pancreatic secretion has been obtained in a normal condition, the fluid has been found to present certain uniform characters. It is viscid, slightly opaline and has a distinctly alkaline reaction. Bernard found the specific gravity of the fluid from the dog to be 1040. The normal fluid from a temporary fistula in a dog has been observed with a specific gravity of 1019 (Flint). The quantity of organic matters in the normal secretion is very great, so that the fluid is completely solidified by heat. This coagulability is one of the properties by which the normal fluid may be distinguished from that which has undergone alteration.

COMPOSITION OF THE PANCREATIC JUICE OF THE DOG (BERNARD).

| | | |
|---|---|---|
| Water | 900 to | 920 |
| Organic matters, precipitable by alcohol and containing always a little lime (amylopsine, trypsine, steapsine etc.) | 90 to | 73·60 |
| Sodium carbonate, Sodium chloride, Potassium chloride, Calcium phosphate | 10 to | 6·40 |
| | 1,000 | 1,000 |

The properties of the organic constituents of the pancreatic juice are distinctive. Although, like albumen, these substances are coagulable by heat, the strong mineral acids and absolute alcohol, they differ from albumen in the fact that their dried alcoholic precipitate can be redissolved in water, giving to the solution the physiological properties of the normal pancreatic secretion. Bernard has also found that they are coagulable by an excess of magnesium sulphate, which will coagulate caseine but has no effect upon albumen. It is important to recognize this distinction between the organic constituents of the pancreatic juice and other nitrogenized substances, especially albumen, from the fact that the last-named substance has the property of forming an imcomplete emulsion with fats. The name pancreatine, given to the organic matter of the pancreatic juice, is inappropriate, as this substance is now known to be composed of several distinct constituents.

A ferment, almost if not quite identical with ptyaline, may be extracted from the normal juice by nearly the same processes as those employed in the isolation of the active principle of the saliva. On account of its vigorous action upon starch, this substance has been called amylopsine.

Trypsine is a ferment capable of acting upon the albuminoids, changing them into peptones. According to Heidenhain, there exists in the secreting cells of the gland a substance called zymogen or more properly, trypsinogen, which, before the secretion is discharged, becomes oxygenated and is changed into trypsine. The action of trypsine on the albuminoids is increased by the addition of small quantities of sodium chloride, sodium glycocholate or sodium carbonate and is diminished by acids.

A substance called steapsine, capable of decomposing fats into fatty acids and glycerine, has been described as one of the organic constituents of the pancreatic juice. This action upon fats, which was described by Bernard, though slight, probably assists in their emulsification.

The inorganic constituents of the pancreatic juice, beyond giving the fluid an alkaline reaction, do not possess any great physiological interest, inasmuch as they do not seem to be essential to its peculiar digestive properties. It has been shown that the organic constituents alone, extracted from the pancreatic juice and dissolved in water, are capable of imparting to the fluid the characters of the normal secretion (Bernard).

The entire quantity of pancreatic juice secreted in the twenty-four hours has been variously estimated by different observers. After what has been said concerning the variations to which the secretion is subject, it is not surprising that these estimates should present great differences. Bernard was able to collect from a dog of medium size eighty to one hundred grains (5·2 to 6·5 grammes) in an hour; but it must be remembered that only one of the ducts was operated upon, and that the gland is very susceptible to irritation. There is no accurate basis for an estimate of the quantity of pancreatic fluid secreted in the twenty-four hours in the human subject or of the quantity necessary for the digestion of a definite quantity of food.

Unlike the gastric juice, the pancreatic juice, under ordinary conditions of heat and moisture, rapidly undergoes decomposition. In warm and stormy weather, the alteration is marked in a few hours; but at a temperature of 50° to 70° Fahr. (10° to 21° C.), the fluid decomposes gradually in two or three days. As it thus undergoes decomposition, the fluid acquires a very offensive, putrefactive odor, and its coagubility diminishes, until finally it is not affected by heat. The alkalinity, however, increases in intensity, and when neutralized with an acid, there is a considerable evolution of carbon dioxide.

*Action of the Pancreatic Juice upon Starches and Sugars.*—The action of the pancreatic juice in transforming starch into sugar was first observed, in 1844, by Valentin, who experimented with an artificial fluid made by infusing pieces of the pancreas in water. Bouchardat and Sandras first noted this property in the normal pancreatic secretion. Amylopsine is undoubtedly the substance concerned in the action of this fluid upon starch.

The property of converting starch into sugar is possessed by several of the digestive fluids. The starchy constituents of food are acted upon by the saliva, and this action is not necessarily arrested as the food, mixed with the saliva, passes into the stomach. The intestinal juice is also capable of effecting the transformation of starch into sugar to a considerable extent. It therefore becomes an important question to determine precisely how far the pancreas is actually concerned in the digestion of this class of substances.

Bernard placed the pancreatic juice at the head of the list of the digestive fluids which act upon starch. This view is correct, although he was in error in claiming that starch is digested almost exclusively by the pancreas. Bernard's experiments, however, were made chiefly on dogs, and these animals do not naturally take starch as food. In man, some of the starchy constituents of the food are acted upon by the saliva, but most of the starch taken as food is digested in the small intestine. Although the intestinal juice is capable of effecting the transformation of starch into sugar, the experimental evidence is conclusive that in this it is subordinate to the pancreatic juice, which latter effects this transformation, at the temperature of the body, with great activity. It is possible that the bile assists in this process to a slight extent. In the transformation of starch into sugar in the small intestine, the same intermediate processes are observed as occur in the action of the saliva; but the change in the intestine into glucose is very rapid. It is stated that amylopsine is not present in the pancreas of the new-born infant (Korowin) and that in early infancy—before the second or third month—the pancreatic extract will not digest starch.

As cane-sugar passes from the stomach into the duodenum, it is almost instantly transformed into glucose. This fact, which has been observed in the lower animals, has received confirmation in the case of intestinal fistula in the human subject, observed by Busch. In this case, when cane-sugar was introduced in quantity into the stomach, fasting, the fluid which escaped from the upper end of the intestine contained a small quantity of glucose, but never any cane-sugar.

It now becomes a question whether the transformation of cane-sugar into glucose be effected by the bile, the intestinal juice or the pancreatic juice. The pancreatic juice and the intestinal juice are the two fluids which might be supposed to have this effect; for it has been repeatedly demonstrated that the bile has of itself but little direct action upon any of the alimentary matters. This point was settled by the experiments of Busch upon the lower end of the intestine, in his case of fistula. Matters introduced into this lower opening came in contact with the intestinal juice only. He found that cane-sugar exposed thus to the action of the intestinal juice was not converted into glucose, but a large portion of it passed unchanged in the fæces.

Out of the body, the pancreatic juice is capable, if kept but for a short time in contact with any of the saccharine principles, of transforming them into lactic acid. The contents of the small intestine are sometimes alkaline or neutral and are sometimes acid. When a very large quantity of sugar has been taken, a part of it may be converted in the intestine into lactic acid, and this may happen with the sugar which results from the digestion of starch; but under ordinary conditions, starch and cane-sugar are readily changed into glucose and are absorbed without undergoing farther transformation.

*Action of the Pancreatic Juice upon Nitrogenized Substances.*—Reference has already been made to the great relative importance of intestinal digestion; and it has been apparent that the process of disintegration of food in the stomach is not final, even as regards many of the nitrogenized substances, but is rather preparatory to the complete liquefaction of these matters, which takes place in the small intestine. In experiments in which the pancreas has been partially destroyed in dogs, there was rapid emaciation, with great voracity, and the passage, not only of unchanged fats and starch, but of undigested nitrogenized matter in the dejections (Bernard). The voracious appetite, progressive emaciation and the passage of all classes of alimentary substances in the fæces, after this operation, indicate the great importance of the pancreatic juice in digestion; but the precise mode of action of this fluid upon the albuminoids is a question of some obscurity. If the bile be shut off from the intestine and discharged externally by a fistulous opening, the same voracity and emaciation are observed; and yet there is no single alimentary substance upon which the bile, of itself, can be shown to exert a very decided digestive action. Farthermore, the pancreatic juice is evidently adapted to act upon alimentary matters after they have been subjected to the action of the stomach, a preparation which is essential to proper intestinal digestion; and once passed into the intestine, the food comes in contact with a mixture of pancreatic juice, intestinal juice and bile. It remains to study, therefore, the special action of the pancreatic secretion upon the albuminoids, as far as this influence can be isolated, and its action in conjunction with the other intestinal fluids and in the presence of other alimentary matters in process of digestion. Nitrogenized alimentary substances, when exposed to the action of the pancreatic juice out of the body, become rapidly softened and dissolved in some of their parts, but soon undergo putrefaction (Bernard). Analogous changes take place in starchy and fatty matters when they are exposed to the action of the pancreatic juice out of the body, and they pass through the various stages of transformation respectively into lactic acid and the fatty acids. Putrefactive action, however, does not readily take place in albuminoids which have been precipitated after having been cooked or in raw gluten or caseine. The presence of fat also interferes with putrefaction; so that Bernard concluded that the fats have an important influence in the intestinal digestion of nitrogenized substances. Experiments made since the observations of Bernard have shown that the ferment of the pancreatic juice concerned in the digestion of albuminoids is trypsine.

Trypsine, in an alkaline medium, changes the albuminoids into their respective peptones, in much the same way and involving nearly the same intermediate conditions as in the digestion of these substances by the gastric juice; but if the action be prolonged, out of the body, the changes continue, and substances are formed which yield leucine, tyrosine and other analogous products. The final putrefactive changes, which result in indol, skatol, phenol etc., some of which have a distinctly fæcal odor, are probably due to the influence of micro-organisms.

Taking into consideration what has been ascertained concerning the action of the pancreatic juice upon the albuminoids, there can be no doubt with regard to the importance of its office in the digestion of these substances after they have been exposed to the action of the gastric juice. Experiments upon the digestion of the albuminoids, after they have passed out of the stomach, show that they undergo important and essential changes as they pass down the intestinal canal. While the bile and the intestinal juice are by no means inert, they seem to be only auxiliary in their action to the pancreatic juice.

The preparation which the albuminoids undergo in the stomach is undoubtedly necessary to the easy digestion, in the small intestine, of that portion which is not dissolved by the gastric juice. This fact has been shown by experiments on intestinal digestion in the inferior animals and by the observations of Busch in the case of intestinal fistula in the human subject.

*Action of the Pancreatic Juice upon Fats.*—The pancreatic juice is the only one of the digestive fluids which is capable of forming a complete and permanent emulsion with fats. The fact that the other digestive fluids will not accomplish this is easily demonstrated as regards the saliva, gastric juice and bile. The intestinal juice is then the only one which might be supposed to have this property. The observations of Busch on this point, in his case of intestinal fistula, are conclusive. He found that fatty matters taken into the stomach were discharged from the upper opening in the intestine in the form of a fine emulsion and were never recognizable as oil; but that fat introduced into the lower intestinal opening was not acted upon and was discharged unchanged in the fæces. The emulsion resulting from the action of pancreatic juice upon fats persists when diluted with water and will pass through a moistened filter, like milk. This does not take place in the imperfect emulsion formed by a mixture of oil with any other of the digestive fluids. Although the normal pancreatic juice is constantly alkaline, this is not an indispensable condition as regards its peculiar action upon fats; for the emulsion is none the less complete when the fluid has been previously neutralized with gastric juice. These facts with regard to the action of the pancreatic juice upon fats were first ascertained by Bernard, in 1848.

A substance called steapsine, extracted from the fresh pancreas, has the property of decomposing fats into the fatty acids and glycerine, but the fatty acids do not appear in the chyle. The emulsification of the fats by the pancreatic juice is to a great extent a mechanical process dependent upon the general physical characters of the fluid; but although the fat which is contained in the lacteal vessels is always neutral, it is thought that steapsine assists in rendering the emulsion fine and permanent.

The cases of fatty diarrhœa connected with disorganization of the pancreas, which were reported by Richard Bright, in 1832, apparently did not direct the attention of physiologists to the uses of this organ. These cases, with others of a similar character which have been reported from time to time, are now brought forward as evidence of the action of the pancreas in the digestion of fats. Many of them presented a train of symptoms analogous to those observed in animals after partial destruction of the gland. The presence of fat in the alvine dejections was marked; and as is now well known, this could be nothing but the undigested fatty constituents of the food. In the three cases observed by Bright, the pancreas was found so disorganized that its secreting action must have been almost if not entirely abolished. In the case reported by Lloyd, the condition was the same; and in the case reported by Elliotson, "the pancreatic duct and the larger lateral branches were filled with white calculi." Another case of disease of the pancreas was described in the catalogue of the Anatomical Museum of the Boston Society for Medical Improvement, in 1847. In this case it was observed by the patient that fatty discharges from the bowels did not take place unless fatty articles of food had been taken. After death a large tumor was found in the situation of the pancreas, but all trace of the normal structure of the organ had been destroyed. Many cases of this character have been quoted by Bernard and others, and they confirm the observations and experiments made upon the lower animals. They all seem to show that the action of the pancreas in digestion is essential to life, but that one of the chief disorders incident to the destruction of this gland relates to the digestion of fats.

Taking into consideration all the facts bearing upon this subject, it is evident that the chief agent in the digestion of fats is the pancreatic juice; and that this fluid acts by forming with the fat a very fine emulsion, thus reducing it to a condition in which it can be absorbed. How far the bile may assist in this process, is a question which will come up for consideration farther on; but the facts with regard to the pancreatic juice are conclusive.

## ACTION OF THE BILE IN DIGESTION.

The physiological anatomy of the liver and the general properties and composition of the bile will be fully considered in connection with the

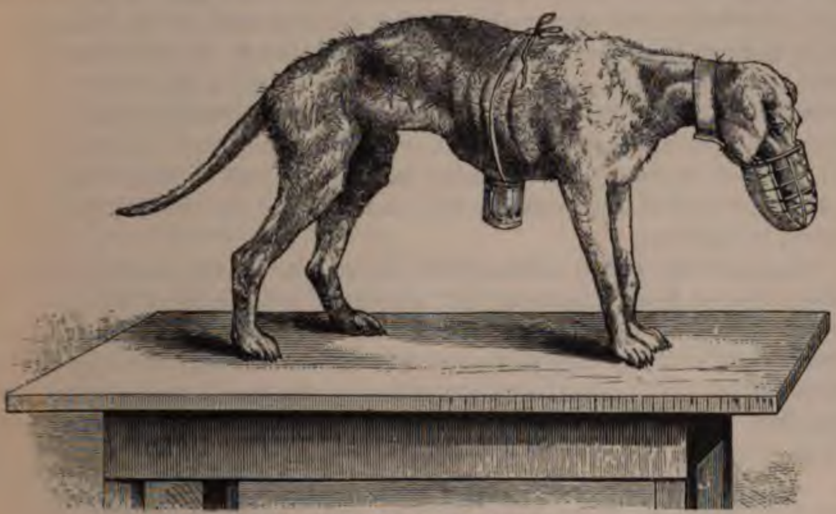

FIG. 77.—*Dog with a biliary fistula.*

From a rough sketch made the fourteenth day after the operation. A small glass vessel is tied around the body to collect the bile, and a wire muzzle, the lower part of which is covered with oil-silk, is placed over the mouth to prevent the animal from licking the bile. The dog is considerably emaciated.

physiology of secretion and excretion; and here it will be necessary only to study the action of the bile in digestion.

The question whether the bile be a purely excrementitious fluid or one concerned in digestion was formerly the subject of much discussion; but it is now admitted by all physiologists that the action of the bile in digestion and absorption, whatever the office of the bile may be as an excretion, is essential to life. The experiments of Swann, Nasse, Bidder and Schmidt, Bernard and others, who have discharged all the bile by a fistula into the gall-bladder, communication between the bile-duct and the duodenum having been cut off, show that dogs operated on in this way have a voracious appetite but die of inanition after having lost four-tenths of the body-weight. The following is an example of experiments of this kind (Flint, 1861): A fistula was made into the gall-bladder of a dog, after excising nearly the whole of the common bile-duct. The animal suffered no immediate effects from the operation, but died at the end of thirty-eight days, having lost 37½ per cent. in weight. He had a voracious appetite, was fed as much as he would eat, was protected from cold and was carefully prevented from licking the bile. During the progress of the experiment, various observations were made on the flow of bile. During the last five or six days, the animal was ravenous but was not allowed to eat all that he would at one time. At that time he was fed twice a day, but he would not eat fat, even when very hungry. During the last day, when too weak to stand, he attempted to eat while lying down.

Human bile is a moderately viscid fluid, of a dark, golden-brown color, an alkaline reaction and a specific gravity of about 1018. Among other constituents, which will be described in connection with the physiology of secretion, it contains sodium united with two acids peculiar to the bile, called glycocholic and taurocholic acids. Sodium taurocholate is much more abundant than the glycocholate. The viscidity of the bile is due to mucus derived in part from the lining membrane of the gall-bladder and in part, probably, from little racemose glands attached to the larger bile-ducts in the substance of the liver. The so-called biliary salts, sodium taurocholate and sodium glycocholate, are probably the constituents of the bile which are concerned in digestion.

Although the bile is constantly discharged in certain quantity into the duodenum, its flow presents marked variations corresponding with certain stages of the digestive process. In fasting animals, the gall-bladder is distended with bile; but in animals opened soon after feeding, it is nearly always found empty. The actual secretion of bile by the liver is also influenced by digestion. The following table gives the variations observed in the dog with a biliary fistula:

TABLE OF VARIATIONS IN THE FLOW OF BILE WITH DIGESTION.

(At each observation the bile was drawn for thirty minutes.)

| Time after feeding. | Fresh bile. | | Dried bile. | | Percentage of dry residue. |
|---|---|---|---|---|---|
| | Grains. | Grammes. | Grains. | Grammes. | |
| Immediately | 8·103 | 0·525 | 0·370 | 0·024 | 4·566 |
| One hour | 20·527 | 1·330 | 0·586 | 0·038 | 2·854 |
| Two hours | 35·760 | 2·317 | 1·080 | 0·070 | 3·023 |
| Four hours | 38·939 | 2·523 | 1·404 | 0·091 | 3·605 |
| Six hours | 22·209 | 1·439 | 0·987 | 0·051 | 4·450 |
| Eight hours | 36·577 | 2·370 | 1·327 | 0·086 | 3·628 |
| Ten hours | 24·447 | 1·584 | 0·833 | 0·054 | 3·407 |
| Twelve hours | 5·710 | 0·370 | 0·247 | 0·016 | 4·325 |
| Fourteen hours | 5·000 | 0·324 | 0·170 | 0·011 | 3·400 |
| Sixteen hours | 8·643 | 0·560 | 0·309 | 0·020 | 3·575 |
| Eighteen hours | 9·970 | 0·646 | 0·277 | 0·018 | 2·778 |
| Twenty hours | 4·769 | 0·309 | 0·170 | 0·011 | 3·565 |
| Twenty-two hours | 7·578 | 0·491 | 0·293 | 0·019 | 3·866 |

Disregarding slight variations in this table, which may be accidental, it may be stated, in general terms, that the bile begins to increase in quantity immediately after eating; that its flow is at its maximum from the second to the eighth hour, during which time the quantity does not vary to any great extent; after the eighth hour it begins to diminish, and from the twelfth hour to the time of feeding it is at its minimum.

One of the uses which has been ascribed to the bile is that of regulating the peristaltic movements of the small intestine and of preventing putrefactive changes in the intestinal contents and the abnormal development of gas; but observations on this point have been somewhat conflicting. During the first few days of the experiment just described, the dejections were very rare; but they afterward became regular, and at one time there was even a tendency to diarrhœa. There can be little doubt, however, that the bile retards the putrefaction of the contents of the intestinal canal, particularly when animal food has been taken. The fæces in the dog with biliary fistula were always extremely offensive. Bidder and Schmidt found this to be the case in dogs fed entirely on meat; but the fæces were nearly odorless when the animals were fed on bread alone. In the case of intestinal fistula in the human subject (Busell), the evacuations which took place after the introduction of alimentary substances into the lower portion of the intestine had an unnaturally offensive and putrid odor. In this case, as it was impossible for matters to pass from the portions of the intestine above the fistula to those below, the food introduced into the lower opening was completely removed from the action of the bile.

It has been shown that the bile of itself has little action upon any of the different classes of alimentary substances. In the fæces of animals with biliary fistula, the only peculiarity which has been observed, aside from the putrefactive odor and the absence of the coloring matter of the bile, has been the presence of an abnormal proportion of fat. This was observed in the fæces of a patient suffering under jaundice apparently due to temporary obstruction of the bile-duct (Flint). The fact was also noted in the dogs experimented upon by Bidder and Schmidt.

The various experiments which have been performed upon animals render it almost certain that the bile has an important influence, either upon the digestion or upon the absorption of fats. Bidder and Schmidt noted, in animals with biliary fistula, that the chyle contained very much less fat than in health. In an animal with a fistula and the bile-duct obliterated, the proportion of fat was 1·90 parts to 1,000 parts of chyle; while in an animal with the biliary passages intact, the proportion was 32·79 parts per 1,000. In animals operated upon in this way there is frequently a great distaste for fatty articles of food. In the observation made in 1861 the dog refused fat meat, even when very hungry and when lean meat was taken with avidity.

Experiments on animals, with regard to the influence of the bile upon the absorption of fats, have resulted in hardly anything definite. It is known, however, that when the bile is diverted from the intestine, the quantity of fat in the chyle is greatly reduced and a large proportion of the fat taken with the food passes through the intestine and is found in the fæces.

The action of the bile in exciting muscular contraction, particularly in the non-striated muscular fibres, is well established. It has been shown by Schiff that this fluid acts upon the muscular fibres situated in the substance of the intestinal villi, causing them to contract, and according to his view, assisting in the absorption of chyle by emptying the lacteals of the villi. The question, however, of the absorption of fats is difficult of investigation. Notwithstanding the obscurity in which this subject is involved, it is certain that the progressive emaciation, loss of strength, and final death of animals deprived of the action of the bile in the intestine, are due to defective digestion and assimilation. Notwithstanding the great quantities of food taken by these animals, the phenomena which precede the fatal result are simply those of starvation. It may be that the biliary salts are absorbed by the blood and are necessary to proper assimilation; but there is no experimental basis for this supposition, and it is impossible to discover these salts in the blood of the portal system by the ordinary tests. It is more probable that the biliary salts influence in some way the digestive process and are absorbed in a modified form with the food.

The observations of Bidder and Schmidt show that the characteristic constituents of the bile are absorbed in their passage down the alimentary canal. Having arrived at an estimate of the quantity of bile daily produced in dogs, they collected and analyzed all the fæcal matter passed by a dog in five days. Of the dry residue of the fæces, the proportion which could by any possibility represent the biliary matters did not amount to one-fourth of the dry residue of the bile which must have been secreted during that time. They also estimated the sulphur contained in the fæces and found that the entire quantity was hardly one-eighth of that which was discharged into the intestine in the bile; and inasmuch as nearly one-half of that found in the fæces came from hairs which had been swallowed by the animal, the experiment showed that nearly all the sulphur contained in the sodium taurocholate had been taken up again by the blood. These observations show that the greater part of the bile, with the biliary salts, is absorbed by the intestinal mucous membrane. Dalton attempted to follow the constituents of the bile into the blood of the portal system, but was unable to detect the biliary salts. Like the peculiar constituents of other secretions which are reabsorbed in the alimentary canal, these substances become changed and are not to be recognized by the ordinary tests, after they are taken into the blood.

While it is the digestion and absorption of fatty substances which seem to be most seriously interfered with in cases of biliary fistula in the inferior animals, the rapid loss of weight and strength show great disturbance in the digestion and absorption of other constituents of food. A fact which indicates a connection between the bile and the process of digestion, is that the flow of this secretion, although constant, is greatly increased when food passes into the intestinal canal.

Although it has been demonstrated that the presence of the bile in the small intestine is necessary to proper digestion and even essential to life, and although the variations in the flow of bile with digestion are now well established, physiologists have but little definite information concerning the exact mode of action of the bile in intestinal digestion and absorption. Nearly all that can be said on this subject is that the action of the bile seems to be auxiliary to that of the other digestive fluids.

## Movements of the Small Intestine.

By the contractions of the muscular coat of the small intestine, the alimentary mass is made to pass along the canal, sometimes in one direction and sometimes in another, the general tendency, however, being toward the cæcum; and the partially digested matters which pass out at the pylorus are prevented from returning to the stomach by the peculiar arrangement of the fibres which constitute the pyloric muscle. Once in the intestine, the food is propelled along the canal by peculiar movements which have been called peristaltic, when the direction is toward the large intestine, and antiperistaltic, when the direction is reversed. These movements are of the character peculiar to the non-striated muscular fibres; viz., slow and gradual, the contraction enduring for a certain time and being followed by a correspondingly slow and gradual relaxation. Both the circular and the longitudinal muscular layers participate in these movements.

Although the mechanism of the peristaltic movements of the intestine may be studied in living animals after opening the abdomen or in animals just killed, the movements thus observed do not entirely correspond with those which take place under natural conditions. In vivisections no movements are observed at first, but soon after exposure of the parts nearly the whole intestine moves like a mass of worms. In the normal process of digestion the movements are never so general or so active. They take place more regularly and consecutively in those portions in which the contents are most abundant, and the movements are generally intermittent, being interrupted by long intervals of repose. In Busch's case of intestinal fistula, there existed a large ventral hernia, the coverings of which were so thin that the peristaltic movements could be readily observed. In this case the general character of the movements corresponded with what has been observed in the inferior animals. It was noted that the movements were not continuous, and that there were often intervals of rest for more than a quarter of an hour. It was also observed that the movements, as indicated by flow of matters from the upper end of the intestine, were intermitted with considerable regularity during part of the night. Antiperistaltic movements, producing discharge of matters which had been introduced into the lower portion of the intestine, were frequently observed.

As far as has been ascertained by observations upon the human subject and warm-blooded animals, the regular intestinal movements are excited by the passage of alimentary matters from the stomach through the tube during the natural process of digestion. By a very slow and gradual action of the muscular coat of the intestine, its contents are passed along, occasionally the action being reversed for a time, until the indigestible residue, mixed with a certain quantity of intestinal secretion, more or less modified, is discharged into the caput coli. These movements are apparently not continuous, and they depend in some degree upon the quantity of matter contained in different parts of the intestinal tract. Judging from the movements in the inferior animals after the abdomen has been opened, the intestines are always changing their position, mainly by the action of their longitudinal muscular fibres, so that the force of gravity does not oppose the onward passage of their contents as much as if the relative position of the parts were constant. There are no definite observations concerning the relative activity of the peristaltic movements in different portions of the intestine; but from the fact that the jejunum is constantly found empty, while the ileum contains a considerable quantity of pultaceous matter, it would seem that the movements must be more vigorous and efficient in the upper portions of the canal.

The gases which are found in the intestine have an important mechanical office. They are useful, in the first place, in keeping the canal constantly distended to the proper degree, thus avoiding the liability to disturbances in the circulation and facilitating the passage of the alimentary mass in obedience to the peristaltic contractions. They also support the walls of the intestine and protect these parts against concussions, in walking, leaping etc. The gases are useful, likewise, in offering an elastic but resisting mass upon which the compressing action of the abdominal muscles may be exerted in straining and in expiration.

There can be hardly any question that the normal movements of the intestine are due principally to the impression made upon the mucous membrane by the alimentary matters, to which is added, perhaps, the stimulating action of the bile. It is difficult to determine with accuracy what part the bile plays in the production of these movements, from the fact that the normal action of the intestine is not easily observed. In the case of intestinal fistula so often referred to, when food was introduced into the lower portion of the canal, there was at first an abundant evacuation every twenty-four hours; but subsequently it became necessary to use enemata. As there was no communication between the lower and the upper portions of the intestine, this fact is an evidence that the peristaltic movements can take place without the action of the bile.

The vigorous peristaltic movements which occur soon after death have been explained in various ways. It has been shown that these movements are not due to a lowering of the temperature or to exposure of the intestines to the air. The latter fact may be easily verified by killing a rabbit, when vigorous movements may be seen through the thin, abdominal walls, even while the cavity is unopened. According to Schiff, the cause of these exaggerated movements is diminution or arrest of the circulation. By compressing the abdominal aorta in a living animal, he was able to excite peristaltic movements in the intestine as vigorous as those which take place after death; and on ceasing the compression, the movements were arrested.

The nerves distributed to the small intestine are derived from the sympathetic and from branches of the pneumogastric, which latter come from the nerve of the right side and are distributed to the whole of the intestinal tract, from the pylorus to the ileo-cæcal valve. The intestine receives no filaments from the left pneumogastric. Throughout the intestinal tract, is a plexus of non-medullated nerve-fibres with groups of nerve-cells, lying between the longitudinal and circular layers of the muscular coat. This is known as Auerbach's plexus. From this plexus, very fine, non-medullated filaments are given off, which form a wider plexus, also with ganglionic cells, situated just beneath the mucous membrane. This is called the plexus of Meissner.

The experiments of Brachet, by which he attempted to prove that the movements of the intestines were under the control of the pneumogastrics and nerves given off from the spinal cord, have not been verified by other observers. The experiments of Müller, however, render it certain that the peristaltic movements are to some extent under the influence of the sympathetic system. In these experiments, movements of the intestine were produced by stimulation of filaments of the sympathetic distributed to its muscular coat, after the ordinary post-mortem movements had ceased. The same results followed the application of potassium hydrate to the semilunar ganglia, the movements reappearing when the agent was applied, " with extraordinary vivacity " in the rabbit, after the abdomen had been opened and the movements had entirely ceased. These experiments have been confirmed by Longet, who found, however, that the movements did not take place unless alimentary matters were contained in the intestine.

The fact that movements occur in portions of intestine cut out of the body and separated, of course, from the nervous system, has led to the view that the peristaltic action is automatic, like the action of the excised heart, and these automatic movements have been attributed to the influence of the ganglia found in the intestinal walls. An analogy between such intestinal movements and the movements of the excised heart seems probable; and a reasonable explanation of this action is afforded by the existence of ganglia in the plexuses of Auerbach and of Meissner.

## Physiological Anatomy of the Large Intestine.

The entire length of the large intestine is about five feet (1·5 metre.) Its diameter is greatest at the cæcum, where it measures, when moderately distended, two and a half to three and a half inches (6·35 to 8·89 centimetres). According to the observations of Brinton, the average diameter of the tube beyond the cæcum is one and two-thirds to two and two-thirds inches (4·23 to 6·77 centimetres). Passing from the cæcum, the canal diminishes in caliber, gradually and very slightly, to where the sigmoid flexure opens into the rectum. This is the narrowest portion of the canal. Beyond this, the rectum gradually increases in diameter, forming a kind of pouch, which abruptly diminishes in size near the external opening, to form the anus.

The general direction of the large intestine is from the cæcum, in the right iliac fossa, to the left iliac fossa, thus encircling the convoluted mass formed by the small intestine, in the form of a horseshoe. From the cæcum to the rectum, the canal is known as the colon. The first division of the colon, called the ascending colon, passes almost directly upward to the under surface of the liver; the canal here turns at nearly a right angle, passes across the upper part of the abdomen and is called the transverse colon; it then passes downward at nearly a right angle, forming the descending colon. The last division of the colon, called the sigmoid flexure, is situated in the left iliac fossa and is in the form of the *italic* letter *S*. This terminates in the rectum, which is not straight, as its name would imply, but presents at least three distinct curvatures, as follows: it passes first in an oblique direction from the left sacro-iliac symphysis to the median line opposite the third piece of the sacrum; it then passes downward in the median line, following the concavity of the sacrum and coccyx; and the lower portion, which is about an inch (2·54 centimetres) in length, turns backward to terminate in the anus.

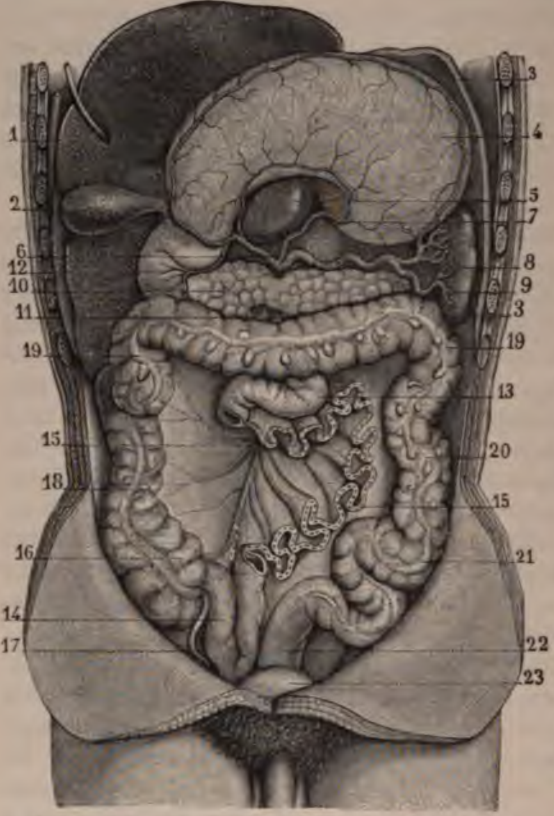


FIG. 78.—*Stomach, pancreas, large intestine etc.* (Sappey).

1, anterior surface of the liver; 2, gall-bladder; 3, 3, section of the diaphragm; 4, posterior surface of the stomach; 5, lobus Spigelii of the liver; 6, cœliac axis; 7, coronary artery of the stomach; 8, splenic artery; 9, spleen; 10, pancreas; 11, superior mesenteric vessels; 12, duodenum; 13, upper extremity of the small intestine; 14, lower end of the ileum; 15, 15, mesentery; 16, *cæcum*; 17, *appendix vermiformis*; 18, *ascending colon*; 19, 19, *transverse colon*; 20, *descending colon*; 21, *sigmoid flexure of the colon*; 22, *rectum*; 23, urinary bladder.

The cæcum, or caput coli, presents a rounded, dilated cavity continuous with the colon above and communicating by a transverse slit with the ileum. At its lower portion is a small, cylindrical tube, opening below and a little posterior to the opening of the ileum, called the vermiform appendix. This is covered with peritoneum and has a muscular and a mucous coat. It is sometimes entirely free and is sometimes provided with a short fold of mesentery for a part of its length. The coats of the appendix are very thick. The muscular coat consists of longitudinal fibres only. The mucous membrane is provided with tubules and closed follicles, the latter frequently being very abundant. This little tube generally contains a quantity of clear, viscid mucus. The uses of the vermiform appendix are unknown.

*Ileo-cæcal Valve.*—The opening by which the small intestine communicates with the cæcum is provided with a valve, known as the ileo-cæcal valve, situated at the inner and posterior portion of the cæcum. The small intestine, at its termination, presents a shallow concavity, which is provided with a horizontal, button-hole slit opening into the cæcum. The surface of the valve which looks toward the small intestine is covered with a mucous membrane provided with villi and in all respects resembling the general mucous lining of the small intestine. Viewed from the cæcum, a convexity is observed corresponding to the concavity upon the other side. The cæcal surface of the valve is covered with a mucous membrane identical with the general mucous lining of the large intestine. It is evident, from an examination of these parts, that pressure from the ileum would open the slit and allow the easy passage of the semi-fluid contents of the intestine; but pressure from the cæcal side approximates the lips of the valve, and the greater the pressure the more firmly is the opening closed. The valve itself is composed of folds formed of the fibrous tissue of the intestine, and circular muscular fibres from both the small and the large intestine, the whole being covered with mucous membrane. The lips of the valve unite at either extremity of the slit and are prolonged on the inner surface of the cæcum, forming two raised bands, or bridles; and these become gradually effaced and are thus continuous with the general lining of the canal. The posterior bridle is a little longer and more prominent than the anterior. These assist somewhat in enabling the valve to resist pressure from the cæcal side. The longitudinal layer of muscular fibres and the peritoneum pass directly over the attached edge of the valve and are not involved in its folds. These give strength to the part, and if they be divided over the valve, gentle traction will suffice to draw out and obliterate the folds, leaving a simple and unprotected communication between the large and the small intestine.

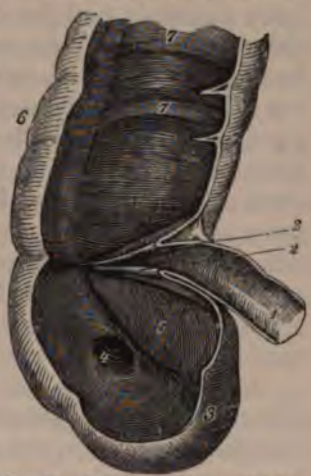


FIG. 79.—*Opening of the small intestine into the cæcum* (Le Bon).
1, small intestine; 2, ileo-cæcal valve; 3, cæcum; 4, opening of the appendix vermiformis; 5, mucous fold at the opening of the appendix; 6, large intestine; 7, 7, folds of the mucous membrane.

*Peritoneal Coat.*—Like most of the other abdominal viscera, the large intestine is covered by peritoneum. The cæcum is covered by this membrane only anteriorly and laterally. It usually is bound down closely to the subjacent parts, and its posterior surface is without a serous investment; although sometimes it is completely covered, and there may be even a short mesocæcum. The ascending colon is likewise covered with peritoneum only in front, and is closely attached to the subjacent parts. The same arrangement is found in the descending colon. The transverse colon is almost completely invested with peritoneum; and the two folds forming the transverse mesocolon separate to pass over the tube above and below, uniting again in front, to form the great omentum. The transverse colon is consequently quite movable. In the course of the colon and the upper part of the rectum, particularly on the transverse colon, are found a number of little, sacculated pouches filled with fat, called the appendices epiploïcæ. The sigmoid flexure of the colon is covered by peritoneum, except at the attachment of the iliac mesocolon. This division of the intestine is quite movable. The upper portion of the rectum is almost completely covered by peritoneum and is but loosely held in place. The middle portion is closely bound down, and is covered by peritoneum only anteriorly and laterally. The lowest portion of the rectum has no peritoneal covering.

*Muscular Coat.*—The muscular fibres of the large intestine have an arrangement quite different from that which exists in the small intestine. The external, longitudinal layer, instead of extending over the whole tube, is arranged in three distinct bands, which begin in the cæcum at the vermiform appendix. Passing along the ascending colon, one of the bands is situated anteriorly, and the others, latero-posteriorly. In the transverse colon the anterior band becomes inferior and the two latero-posterior bands become respectively postero-superior and postero-inferior. In the descending colon and the sigmoid flexure the muscular bands resume the relative position which they had in the ascending colon. As these longitudinal fibres pass to the rectum, the anterior and the external bands unite to pass down on the anterior surface of the canal, while the posterior band passes down on its posterior surface. Thus the three bands here become two. These two bands as they pass downward, though remaining distinct, become much wider; and longitudinal muscular fibres beginning at the rectum are situated between them, so that this part of the canal, especially in its lower portion, is covered with longitudinal fibres in a nearly uniform layer.

*Mucous Coat.*—The mucous lining of the large intestine presents several important points of difference from the corresponding membrane in the small intestine. It is paler, somewhat thicker and firmer, and is more closely adherent to the subjacent parts. In no part of this membrane are there any folds, like those which form the valvulæ conniventes of the small intestine; and the surface is smooth and free from villi.

Throughout the entire mucous membrane, from the ileo-cæcal valve to the anus, are orifices which lead to simple follicular glands. These structures resemble in all respects the follicles of the small intestine, except that they are a little longer, owing to the greater thickness of the membrane, are wider and rather more abundant. Among these small follicular openings are found, scattered irregularly throughout the membrane, larger openings which lead to utricular glands, resembling the closed follicles, in general structure, except that they have an orifice opening into the cavity of the intestine, which is sometimes so large as to be visible to the naked eye. The number of these glands is very variable, and they exist throughout the intestine, together with the closed follicles, except in the rectum. In the cæcum and colon, isolated closed follicles are generally found, which are identical in structure with the solitary glands of the small intestine. These are very variable, both in number and size.

The mucous membrane of the rectum, in the upper three-fourths of its extent, does not differ materially from that of the colon. In the lower fourth, the fibrous tissue by which the lining membrane is united to the subjacent muscular coat is loose, and the membrane, when the canal is empty, is thrown into a great number of irregular folds. At the site of the internal sphincter, five or six little, semilunar valves have been observed, with their concavities directed toward the colon. These form an irregular, festooned line, which surrounds the canal; their folds, however, are small and have no tendency to obstruct the passage of fæcal matters. The simple follicles are particularly abundant in the rectum, and the membrane is constantly covered with a thin coating of mucus. Another peculiarity to be noted in the mucous membrane of the lower portion of the rectum is its great vascularity, the veins, especially, being very abundant.

The rectum terminates in the anus, a button-hole orifice, situated a little in front of the coccyx, which is kept closed and somewhat retracted, except during the passage of the fæces, by the powerful external sphincter. This muscle is composed entirely of striated fibres, which are arranged in the form of an ellipse, its long diameter being antero-posterior.

It is now almost universally admitted that the digestion of all classes of alimentary substances is completed either in the stomach or in the small intestine, and that the mucous membrane of the large intestine does not secrete a fluid endowed with any well marked digestive properties. The simple follicles, the closed follicles, and the utricular glands, produce a glairy mucus, which, as far as is known, serves merely to lubricate the canal. This has never been obtained in sufficient quantity to admit of any accurate investigation into its properties.

In studying the changes which the alimentary mass undergoes in its passage through the small intestine, it has been seen that in this portion of the canal, the greatest part of all the nutritive material is not only liquefied but is absorbed. Sometimes fragments of muscular fibre, oil-globules, and other matters in a state of partial disintegration, may be detected in the fæces; but generally this is either the result of the ingestion of an excessive quantity of these substances or it depends upon some derangement of the digestive apparatus. When intestinal digestion takes place with regularity, the transformation of the alimentary residue into fæcal matter is slow and gradual. As the contents of the stomach are passed little by little into the duodenum, the mass becomes of a bright-yellow color, and its fluidity is increased, from the admixture of bile and pancreatic fluid. In passing along the canal, the consistence of the mass gradually diminishes on account of absorption of its liquid portions, and the color becomes darker; and by the time that the contents of the ileum are ready to pass into the cæcum, the greatest part of those substances recognized as alimentary has become changed and absorbed. The various forms of starchy and saccharine matters, unless they have been taken in excessive quantity, soon disappear from the intestine; and the glucose, which is the result of their digestion, may be recognized in the portal blood. As a rule, fatty matters are not found in the lower part of the ileum, having passed into the lacteals, in the form of an emulsion. Neither fibrin, albumen nor caseine, can be detected in the ileum; and the muscular substance, as recognized by its microscopical characters, becomes gradually disintegrated and is lost—except a few isolated fragments deeply colored with bile—some time before the indigestible residue passes into the large intestine.

In the human subject those portions of the food which resist the successive and combined action of the different digestive secretions are derived chiefly from the vegetable kingdom. Hard, vegetable seeds, the cortex of the cereals, spiral vessels, and, indeed, all parts which are composed largely of cellulose, pass through the intestinal canal without much change. These substances form, in the fæces, the greatest part of what can be recognized as the residue of matters taken as food. It is well known that an exclusively animal diet, particularly if the nutritious matters be taken in a concentrated and readily assimilable form, leaves very little undigested matter to pass into the large intestine, and gives to the fæces a character quite different from that which is observed in herbivorous animals or in man when subjected to an exclusively vegetable diet. The characters of the residue of the digestion of albuminoid substances are not very distinct. As a rule, none of the albuminoids are to be recognized in the healthy fæces by the ordinary tests.

Absorption of various articles of food in a liquid form may take place with great activity in the large intestine, although it has not been shown that the secretions in this part of the alimentary canal have any distinct digestive properties; still, as is shown in rectal alimentation, eggs, milk and meat-extracts may be taken up by the mucous membrane, and they enter the circulation in such a form that they contribute to the nutrition of the body.

*Processes of Fermentation in the Intestinal Canal.*—The processes of fermentation in the intestines are not properly digestive and are to a great extent due to the action of micro-organisms, which exist here in great numbers and variety. It is possible, however, that future researches may show that micro-organisms play an important part in actual digestion, as is foreshadowed in a recent article by Pasteur (August, 1887). Pasteur has isolated seventeen different micro-organisms of the mouth. Some of these dissolved albumen, gluten and caseine, and some transformed starch into glucose. The micro-organisms described were not destroyed by the action of the gastric juice. These observations are very suggestive, and they seem to open a new field of inquiry as regards certain of the processes of digestion. Most of the fermentations in the small intestine are either putrefactive or of a nature analogous to fermentation, and the processes are continued with increased activity in the large intestine.

Some of the substances resulting from intestinal fermentations have already been described. Indol, skatol, phenol etc., seem to be produced by the action of micro-organisms; but the effect of these products is to kill the micro-organisms and thus to limit the putrefactive processes. The production of indol, skatol and phenol is arrested by the action of certain drugs, such as calomel, salicylic acid and other so-called antiseptics. The fermentive changes in the intestines involve the production of certain gases, which will be described at the close of this chapter.

### Contents of the Large Intestine.

When the contents of the small intestine have passed the ileo-cæcal valve, they become changed in their general character, partly from admixture with the secretions of this portion of the canal, and are then known as the fæces. The most notable changes relate to consistence, color and odor. The odor, especially, of normal fæcal matter is characteristic.

Fæcal matter has a much firmer consistence than the contents of the ileum, which is due to a constant absorption of the liquid portions. As a rule, the consistence is great in proportion to the length of time that the fæces remain in the large intestine; and this is variable in different persons, and in the same person, in health, depending somewhat upon the character of the food. The color changes from the yellow, more or less bright, which is observed in the ileum, to the dark yellowish-brown characteristic of the fæces. Although the bile-pigment can not usually be recognized by the ordinary tests, it is this which gives to the contents of the large intestine their peculiar color, which is lost when the bile is not discharged into the duodenum. In a specimen of healthy human fæces, which had been dried, extracted with alcohol, the alcoholic extract precipitated with ether and the precipitate dissolved in distilled water, it was impossible to detect the biliary salts by Pettenkofer's test. In a watery extract of the same fæces, the addition of nitric acid failed to show the reaction of the coloring matter of the bile (Flint, 1862). The color of the fæces, however, varies considerably under different forms of diet. With a mixed diet the color is yellowish-brown; with an exclusively flesh-diet it is much darker; and with a milk-diet it is more yellow (Wehsarg).

The odor of the fæces, which is characteristic and quite different from that of the contents of the ileum, is variable and is due in part to the peculiar decomposition of the residue of the food, in part to the decomposition of the bile and in part to matters secreted by the mucous membrane of the colon and of the glands near the anus.

The entire quantity of fæces in the twenty-four hours, according to Wehsarg, is about 4·6 ounces (128 grammes). This was the mean of seventeen observations; the largest quantity being 10·8 ounces (306 grammes), and the smallest, 2·4 ounces (68 grammes).

The reaction of the fæces is variable, depending chiefly upon the character of the food. Marcet found the human excrements always alkaline. Wehsarg, on the other hand, found the reaction generally acid, but very frequently it was alkaline or neutral.

The proportions of water and solid matter in the fæces are variable. Berzelius found in the healthy human fæces, 73·3 parts of water and 26·7 parts of solid residue. The average of seventeen observations by Wehsarg was precisely the same. In the observations of Wehsarg, the mean quantity of solid matter discharged in the fæces in the twenty-four hours was 463 grains (30 grammes), the extremes being 882·8 grains (57·2 grammes), and 251·6 grains (16·28 grammes). The proportion of undigested matters in the solid residue was very small, averaging but little more than ten per cent., the mean quantity in the twenty-four hours in ten observations being but 52·5 grains (3·4 grammes). This was found, however, to be very variable; the largest quantity being 126·5 grains (8·2 grammes), and the smallest, 12·5 grains (0·81 gramme).

Microscopical examination of the fæces reveals various vegetable and animal structures which have escaped the action of the digestive fluids. Wehsarg also found a "finely divided fæcal matter" of indefinite structure, but containing partly disintegrated intestinal epithelium. Crystals of cholesterine were never observed. Whenever the matter is neutral or alkaline, crystals of ammonio-magnesian phosphate are found. Mucus is also found in variable quantity in the fæces, with desquamated epithelium and a few leucocytes. In addition, recent microscopical researches have shown the presence of spores of yeast and a great variety of bacteria, which latter exist in the fæces in great abundance. These organisms probably excite many of the so-called putrefactive changes in the intestinal contents, which result in the formation of indol, phenol, skatol, cresol etc. According to Senator, these putrefactive products do not occur in the meconium. The quantity of inorganic salts in the fæces is not great. In addition to the ammonio-magnesian phosphate, magnesium phosphate, calcium phosphate and a small quantity of iron have been found. The chlorides are either absent or are present only in small quantity.

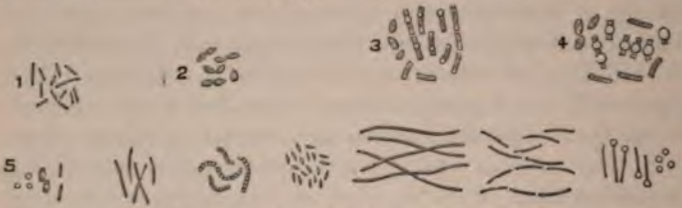


FIG. 80.—*Micro-organisms of the large intestine* (Landois).
1, bacterium coli commune; 2, bacterium lactis aërogenes; 3, 4, the large bacilli of Bienstock, with partial endogenous spore-formation; 5, the various stages of the development of the bacillus which causes the fermentation of albumen.

Marcet has pretty generally found in the human fæces a substance possessing the characters of margaric acid, and volatile fatty acids; the latter free, however, from butyric acid. He also found a coloring matter, which is probably a modification of bile-pigment. Cystine is mentioned as an occasional constituent of the fæces.

In addition to the matters just enumerated, the following substances have been extracted from the normal fæces:

*Excretine and Excretoleic Acid.*—Excretine was obtained from the normal fæces, by Marcet, in 1854. This substance crystalizes from an ethereal solution in two or three days, in the form of long, silky crystals. Examined with the microscope, these are found to consist of acicular, four-sided prisms of variable size. Excretine is insoluble in water, slightly soluble in cold alcohol, but very soluble in ether and in hot alcohol. Its alcoholic solutions are faintly though distinctly alkaline. Its fusing-point is between 203° and 205° Fahr. (95° and 96° C.). It may be boiled with potassium hydrate for hours without undergoing saponification. The quantity of excretine contained in the fæces is not large. Only 12·6 grains (0·816 gramme) were obtained by Marcet from nine evacuations.

There exists very little definite information concerning the production of excretine. Marcet examined on one occasion the contents of the small intestine of a man who had died of disease of the heart, without finding any excretine. It is probable that this substance is formed in the large intestine, although farther observations are wanting on this point.

The substance called excretoleic acid is very indefinite in its composition and properties. It is described as an olive-colored, fatty acid, insoluble in water, non-saponifiable, and very soluble in ether and in hot alcohol. It fuses between 77° and 79° Fahr. (25° and 26·11° C.).

*Stercorine.*—This substance, discovered in the fæces in 1862 (Flint), was described by Boudet in 1833, as existing in minute quantity in the serum of the blood, and was called seroline. As it is one of the most abundant and characteristic constituents of the stercoraceous matter, it may properly be called stercorine, particularly as observations have led to the opinion that it really does not exist in the serum, but is formed from cholesterine by the processes employed for its extraction from the blood (Flint).

Stercorine may be extracted in the following way: The fæces are first evaporated to dryness, pulverized and treated with ether. The ether-extract is then passed through animal charcoal, fresh ether being added until the original quantity of the ether-extract has passed through. It is impossible to entirely decolorize the solution by this process; but it should pass through perfectly clear and of a pale-amber color. The ether is then evaporated and the residue is extracted with boiling alcohol. This alcoholic solution is evaporated, and the residue is treated with a solution of potassium hydrate for one or two hours at a temperature a little below the boiling-point, by which all the saponifiable fats are dissolved. The mixture is then largely diluted with water, thrown upon a filter, and washed until the fluid which passes through is neutral and perfectly clear. The filter is then dried and the residue is washed out with ether. The ether-solution is then evaporated, extracted with boiling alcohol, and the alcoholic solution is evaporated. The residue of this last evaporation is pure stercorine.

When first obtained, stercorine is a clear, slightly amber, oily substance, of about the consistence of Canada balsam used in microscopical preparations. In four or five days it begins to show the characteristic crystals. These are few in number at first, but soon the entire mass assumes a crystalline form. In one analysis, from seven and a half ounces (202·5 grammes) of normal human fæces (the entire quantity for the twenty-four hours), 10·417 grains (0·675 gramme) of stercorine were obtained, the extract consisting entirely of crystals. This was all the stercorine to be extracted from the regular, daily evacuation of a healthy male twenty-six years of age and weighing about one hundred and sixty pounds (72·58 kilos.). In the absence of other investigations, the daily quantity of this substance excreted may be assumed to be not far from ten grains (0·648 gramme).

In many regards stercorine bears a close resemblance to cholesterine. It is neutral, inodorous, and insoluble in water and in a solution of potassium hydrate. It is soluble in ether and in hot alcohol, but is almost insoluble in cold alcohol. A red color is produced when it is treated with strong sulphuric acid. It may be easily distinguished from cholesterine, however, by the form of its crystals. It fuses at a low temperature, 96·8° Fahr. (36° C.), while cholesterine fuses at 293° Fahr. (145° C.).

Stercorine crystallizes in the form of thin, delicate needles, frequently mixed with clear, rounded globules, which are probably composed of the same substance in a non-crystalline form. When the crystals are of considerable size, the borders near their extremities are split longitudinally for a short distance. The crystals are frequently arranged in bundles. They are not to be confounded with excretine, which crystallizes in the form of regular, four-sided prisms, or with the thin, rhomboidal or rectangular tablets of cholesterine. They are identical with the crystals of seroline, figured by Robin and Verdiel.

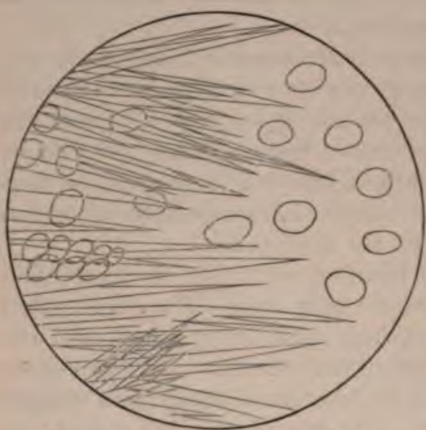

FIG. 81.—*Stercorine from the human fæces.*

There can be no doubt with regard to the origin of the stercorine which exists in the fæces. Whenever the bile is not discharged into the duodenum, as is probably the case for a time in icterus accompanied with clay-colored evacuations, stercorine is not to be discovered in the dejections. In one case of this kind, in which the fæces were subjected to examination, the matters extracted with hot alcohol were entirely dissolved by boiling for fifteen minutes with a solution of potassium hydrate, showing the absence of cholesterine and stercorine. In another examination of the fæces from this patient, made nineteen days after, when the icterus had almost entirely disappeared and the evacuations had become normal, stercorine was discovered. These facts show that the cholesterine of the bile, in its passage through the intestine, is changed into stercorine. Both of these substances are crystallizable, non-saponifiable, are extracted by the same chemical manipulations, and behave in the same way when treated with sulphuric acid. Stercorine must be regarded as a modification of cholesterine, which is the excrementitious constituent of the bile.

The change of cholesterine into stercorine is directly connected with the process of intestinal digestion. If an animal be kept for some days without food, cholesterine will be found in the fæces, although, for a few days, stercorine is also present. It is a fact generally recognized by those who have analyzed the fæces, that cholesterine does not exist in the normal evacuations; but whenever digestion is arrested, the bile being constantly discharged into the duodenum, cholesterine is found in large quantity. For example, in hibernating animals, cholesterine is always present in the fæces. The same is true of the contents of the intestines during fœtal life; the meconium always containing a large quantity of cholesterine, which disappears from the evacuations when the digestive function becomes established. Stercorine has not been subjected to ultimate analysis. Its physiological relations will be considered in connection with the excretory office of the liver.

*Indol, Skatol, Phenol etc.*—The so-called putrefactive processes, which begin in the small intestine, are more marked in the large intestine and give rise to certain products which have the characteristic fæcal odor. Certain of these substances may be produced by the prolonged action, out of the body, of the pancreatic juice upon albuminoids. The pancreatic juice, in an alkaline medium, changes the trypsine-peptones into leucine, tyrosine, hypoxanthine and asparaginic acid. By still farther prolonging this action, indol ($C_8H_7N$), skatol ($C_9H_9N$) and phenol ($C_6H_6O$), with some other analogous substances and volatile fatty acids, are formed, and there is an evolution of certain gases. It is probable that these products are formed in abnormal quantities in the small intestine in certain cases of intestinal dyspepsia. The relations of the substances just mentioned to the general process of nutrition are not understood.

*Movements of the Large Intestine.*—Movements of the general character noted in the small intestine occur in the large intestine, although the peculiarities in the arrangement of the muscular fibres and the more solid consistence of the contents render these movements in the large intestine somewhat distinctive. In all instances where the movements have been observed in the human subject or in the lower animals, they have been found to be less vigorous and rapid than the contractions of the small intestine. Indeed, when the abdominal organs are exposed, either in a living animal or immediately after death, movements of the large intestine are generally not observed, except on the application of mechanical or electric stimulation; and they are then more circumscribed and much less marked than in any other part of the alimentary canal. That the fæces remain for a considerable time in some of the sacculated pouches of the colon, is evident from the appearance which they sometimes present of having been moulded to the shape of the canal. This appearance is frequently observed in the dejections, which are then said to be "figured."

In the cæcum, the pressure of matters received from the ileum forces the mass onward into the ascending colon, and the contractions of its muscular fibres are probably slight and inefficient. Once in the colon, it is easy to see how the contractions of the muscular structure—the longitudinal bands shortening the canal, and the transverse fibres contracting below and relaxing above—are capable of passing the fæcal mass slowly onward. Although the transverse fibres are thin and apparently of little power, their contraction is undoubtedly sufficient to empty the sacculi, when assisted by the movements of the longitudinal fibres, especially as the canal is never completely filled and the fæces are frequently in the form of small, moulded lumps. By these slow and gradual movements, the contents of the large intestine are passed toward the sigmoid flexure of the colon, where they are arrested until the period arrives for their final discharge. The time occupied in the passage of the fæces through the ascending, transverse and descending colon is undoubtedly variable in different persons, as great variations are observed in the intervals between the acts of defæcation. During their passage along the colon, the contents of the canal assume more and more of the normal fæcal consistence and odor and become slightly coated with the mucous secretion of the parts.

The accumulation of fæces generally takes place in the sigmoid flexure of the colon; and under normal conditions, the rectum is found empty and contracted. This part of the colon is much more movable than other portions of the large intestine. At certain tolerably regular intervals, the fæcal matter is passed into the rectum and is then almost immediately discharged from the body.

*Defæcation.*—In health, expulsion of fæcal matters takes place with regularity generally once in the twenty-four hours. This rule, however, is by no means invariable, and dejections may habitually occur twice in the day or every second or third day, within the limits of health. At the time when defæcation ordinarily takes place, a peculiar sensation is experienced calling for an evacuation of the bowels; and if this be disregarded, the desire may pass away, after a little time the act becoming impossible. It is probable that the fæces are then passed out of the rectum by antiperistaltic action.

The condition which immediately precedes the desire for defæcation is probably the descent of the contents of the sigmoid flexure of the colon into the rectum. It was formerly thought that the fæces constantly accumulated in the dilated portion of the rectum, where they remained until an evacuation took place; but the arguments of O'Beirne against such a view are conclusive. He demonstrated, by explorations in the human subject, that under ordinary conditions, the rectum is contracted and contains neither fæces nor gas. It is, indeed, a fact familiar to every surgeon, that the rectum usually contains nothing which can be reached by the finger in physical examinations, and that paralysis or section of the muscles which close the anus by no means involves, necessarily, a constant passage of fæcal matter. O'Beirne not only found the rectum empty and presenting a certain degree of resistance to the passage of injected fluids, but on passing a stomach-tube into the bowel, after penetrating six to eight inches (15 to 20 centimetres), it passed into a space in which its extremity could be moved with great freedom, and there was instantly a rush of flatus, of fluid fæces, or of both, through the tube. In some instances in which nothing escaped through the tube, the instrument conveyed to the hand an impression of having entered a solid mass; and on being withdrawn it contained solid fæces in its upper portion. The sensation which leads to an effort to discharge the fæces is due to the accumulation of matters in the sigmoid flexure, which finally present at the contracted, upper portion of the rectum. This constriction, situated at the most superior portion of the rectum, is sometimes called the sphincter of O'Beirne.

The above is the mechanism of the descent of fæcal matter into the rectum in defæcation, as the act is usually performed; but under certain conditions, fæces must accumulate in the dilated portion of the rectum. Ordinarily, the discharge of fæces takes place only after the efforts have been continued for a certain time, and when the evacuation is "figured," the whole length discharged frequently exceeds so much the length of the rectum, that it is evident that a portion of it must have come from the colon; but in cases in which the fæces are very fluid, or when the call for an evacuation has not been regarded and has become imperative, the immediate discharge of matters when the sphincter is relaxed shows that the rectum has been more or less distended.

In the process of defæcation, the first act is the passage, by peristaltic contractions, of the contents of the sigmoid flexure of the colon through the slightly constricted opening of the rectum into its dilated portion below. The fæcal matter, however, is not allowed to remain in this situation, but it passes into the lower portion of the rectum, in obedience to the contractions of its muscular coat, assisted by the action of the abdominal muscles and the diaphragm. The circular fibres of the rectum undergo the ordinary peristaltic contraction; and the action of the longitudinal fibres is to render the rectum shorter and more nearly straight. The internal and the external sphincters present a certain resistance to the discharge of the fæces, particularly the external sphincter, which is a striated muscle of considerable power. There is always, however, a voluntary relaxation of this muscle, or rather a cessation of its semi-voluntary contraction, which immediately precedes the expulsive act. The dilatation of the anus is also facilitated by the action of the levator ani, which arises from the posterior surface of the body and ramus of the pubis, the inner surface of the spine of the ischium, and a line of fascia between these two points, passes downward, and is inserted into the median raphe of the perineum and the sides of the rectum, the fibres uniting with those of the sphincter. While this muscle forms a support for the pelvic organs during the act of straining, it steadies the end of the rectum, and by its contractions, favors the relaxation of the sphincter and draws the anus forward.

The diaphragm and the abdominal muscles merely compress the abdominal organs, and consequently those contained in the pelvis, and assist in the expulsion of the contents of the rectum. The diaphragm is the most important of the voluntary muscles concerned in this process; and during the act of straining, the lungs are moderately filled and respiration is interrupted. The vigor of these efforts depends greatly upon the consistence of the fæcal mass, very violent contractions being frequently required for the expulsion of hardened fæces after long constipation. Although more or less straining generally takes place, the contractions of the muscular coats of the rectum frequently are competent of themselves to expel the fæces, especially when they are soft.

By a combination of the movements above described, the floor of the perineum is pressed outward, the anus is dilated, the sharp bend in the lower part of the rectum is brought more into line with the rest of the canal, and a portion of the contents of the rectum is expelled. Very soon, however, the passage of fæces is interrupted by a contraction of the levator ani and the sphincter, by which the anus is suddenly and rather forcibly retracted. This muscular action may be effected voluntarily; but after the sphincter has been dilated for a time, the evacuation is interrupted in this way, notwithstanding all efforts to oppose it. After a time, another portion of fæces is discharged, until the matters have ceased to pass out of the sigmoid flexure and the rectum has been emptied.

Very little need be said concerning the influence of the nervous system on the movements concerned in defæcation. The non-striated muscular fibres which form the muscular coat of the rectum are supplied with nerves from the sympathetic system; and to the external sphincter are distributed filaments from the last sacral pair of spinal nerves. These nerves bring the sphincter in a certain degree under the control of the will, and impart likewise the property of tonic contraction, by which the anus is kept constantly closed. The nerve-centre for defæcation in the dog, or the ano-spinal centre, is in the spinal cord, at the site of the fifth lumbar vertebra (Budge).

### Gases found in the Alimentary Canal.

The gases in the stomach appear to have no definite office. They generally exist in very small quantity and they are sometimes absent. The oxygen and nitrogen are derived from the little bubbles of air which are incorporated with the alimentary bolus during mastication and insalivation. The other gases are probably evolved from the food during digestion; at least, there is no satisfactory evidence that they are produced in any other way. Magendie and Chevreul collected and analyzed a small quantity of gas from the stomach of an executed criminal a short time after death and ascertained that it had the following composition:

GASES CONTAINED IN THE STOMACH.

| | |
|---|---|
| Oxygen | 11·00 |
| Carbon dioxide | 14·00 |
| Pure hydrogen | 3·55 |
| Nitrogen | 71·45 |
| | 100·00 |

Magendie and Chevreul found three different gases in the small intestine. Their examinations were made upon three criminals soon after execution. The first was twenty-four years of age, and two hours before execution, he had eaten bread and Gruyère cheese and had drunk red wine and water. The second, who was executed at the same time, was twenty-three years of age, and the conditions as regards digestion were the same. The third was twenty-eight years of age, and four hours before death, he ate bread, beef and lentils, and drank red wine and water. The following was the result of the analyses:

GASES CONTAINED IN THE SMALL INTESTINE.

| | First criminal. | Second criminal. | Third criminal. |
|---|---|---|---|
| Carbon dioxide | 24·39 | 40·00 | 25·00 |
| Pure hydrogen | 55·53 | 51·15 | 8·40 |
| Nitrogen | 20·08 | 8·85 | 66·60 |
| | 100·00 | 100·00 | 100·00 |

No oxygen was found in either of the examinations, and the quantities of the other gases were so variable as to lead to the supposition that their proportion is not at all definite. Reference has already been made to the mechanical office of these gases in intestinal digestion.

In the large intestine, the constitution of the gases presented the same variability as in the small intestine. Carburetted hydrogen was found in all of the analyses. In the large intestine of the first criminal and in the rectum of the third, were found traces of hydrogen monosulphide. The following is the result of the analyses in the cases just cited. In the third, the gaseous contents of the cæcum and the rectum were analyzed separately:

GASES CONTAINED IN THE LARGE INTESTINE.

| | First criminal. | Second criminal. | Third criminal. | Third criminal. |
|---|---|---|---|---|
| | | | Cæcum. | Rectum. |
| Carbon dioxide | 43·50 | 70·00 | 12·50 | 42·86 |
| Carburetted hydrogen and traces of hydrogen monosulphide | 5·47 | ..... | ..... | ..... |
| Pure hydrogen and carburetted hydrogen | ..... | 11·60 | ..... | 11·18 |
| Pure hydrogen | ..... | ..... | 7·50 | ..... |
| Carburetted hydrogen | ..... | ..... | 12·50 | ..... |
| Nitrogen | 51·03 | 18·40 | 67·50 | 45·96 |
| | 100·00 | 100·00 | 100·00 | 100·00 |

*Origin of the Intestinal Gases.*—The most reasonable view to take of the origin of the gases normally found in the intestines is that they are given off from the articles of food in their various stages of digestion and decomposition. That this is the principal source of the intestinal gases, there can be no doubt; and it is well known that certain articles of food, particularly vegetables, generate much more gas than others. The principal gases found in the intestinal canal may all be obtained from the food. Some of them, as hydrogen and carburetted hydrogen, do not exist in the blood; and it is difficult to conceive how they can be generated in the intestine except by decomposition of certain of the articles of food. Gases do not exist in the alimentary canal of the fœtus.

## CHAPTER X.

### *ABSORPTION—LYMPH AND CHYLE.*

Absorption by blood-vessels—Absorption by lacteal and lymphatic vessels—Physiological anatomy of the lacteal and lymphatic vessels—Lymphatic glands—Absorption by the lacteals—Absorption by the skin—Absorption by the respiratory surface—Absorption from closed cavities, reservoirs of glands, etc.—Absorption of fats and insoluble substances—Variations and modifications of absorption—Mechanism of the passage of liquids through membranes—Lymph and chyle—Properties and composition of lymph—Origin and uses of the lymph—Composition of the chyle—Microscopical characters of the chyle—Movements of the lymph and chyle.

DIGESTION has two great objects: one is to liquefy the different alimentary substances; and the other, to begin the series of transformations by which these are rendered capable of nourishing the organism. The matters thus acted upon are taken into the blood as fast as the requisite changes in their constitution are effected; and once received into the circulation, they become part of the nutritive fluid, supplying the loss which the constant regeneration of the tissues from matters furnished by the blood necessarily involves. The only constituents of food which possibly do not obey this general law, as regards their absorption, are the fats. Although a small portion of the fat taken as food may pass directly into the blood-vessels of the intestinal canal, by far the greatest part finds its way into the circulation by means of special absorbent vessels which empty into large veins. In whatever way fat enters the blood, it is not dissolved but is reduced to the condition of a fine emulsion.

### ABSORPTION BY BLOOD-VESSELS.

That substances in solution can pass through the walls of the capillaries and of the small veins, and that absorption actually takes place in great part by blood-vessels, are facts which hardly demand discussion at the present day. Soluble substances which have disappeared from the alimentary canal have been repeatedly found in the blood coming from this part, even when the lymphatics have been divided and communication existed only through the blood-vessels; and it has been shown that during absorption, the blood of the portal vein is rich in albuminoids, sugar and other matters resulting from digestion.

In the mouth and œsophagus, the sojourn of alimentary matters is so brief and the changes which they undergo are so slight, that no considerable absorption can take place. It is evident, however, that the mucous membrane of the mouth is capable of absorbing certain soluble matters, from the effects which are constantly observed when the smoke or the juice of tobacco is retained in the mouth, even for a short time. In the stomach, however, absorption takes place with great activity. A large proportion of the ingested liquids and of those constituents of food which are dissolved by the gastric juice and converted into peptones is taken up directly by the blood-vessels of the stomach. It may, indeed, be assumed, as a general law, that alimentary matters are in great part absorbed as soon as their digestive transformations in the alimentary canal have been completed.

In the passage of the food along the intestinal canal, as the digestion of the albuminoids is completed, these matters are absorbed, and their passage into the mass of blood is indicated by an increase in its proportion of albuminoid constituents. The greatest part of the food is absorbed by the intestinal mucous membrane, and with the alimentary substances proper, a large quantity of secreted fluid is reabsorbed. This fact is particularly marked as regards the bile. The biliary salts disappear as the alimentary mass passes down the intestine, and undoubtedly are absorbed, although they are so changed that they can not be detected in the blood by the ordinary tests. In this portion of the alimentary canal, it will be remembered, an immense absorbing surface is provided by the arrangement of the mucous membrane in folds, forming the valvulæ conniventes, and by the presence of villi, which are found throughout the small intestine. A certain portion of the gaseous contents of the intestines is also taken up, although it is not easily ascertained what particular gases are thus absorbed.

### Absorption by Lacteal and Lymphatic Vessels.

The history of the discovery of what is ordinarily termed the absorbent system of vessels, from the vague allusions of Hippocrates, Galen, Aristotle and others, to the description of the thoracic duct in the middle of the sixteenth century, by Eustachius, and finally to the discovery of the lacteals by Asellius, in 1622, is more interesting in an anatomical than in a physiological point of view. The history of the anatomy of the absorbent system dates from the discovery of the thoracic duct; but from the discovery of the lacteals, by Asellius, dates the history of these vessels as the carriers of nutritive matters from the intestinal canal to the general system.

In 1649, Pecquet discovered the receptaculum chyli and demonstrated that the lacteals did not pass to the liver, but emptied the chyle into the thoracic duct, by which it is finally conveyed into the venous system. In 1650–'51, the anatomical history of the absorbent vessels was completed by the discovery, by Rudbeck, of vessels carrying a colorless fluid, in the liver and finally in almost all parts of the body. Rudbeck demonstrated the anatomical identity of these vessels with the lacteals. They were afterward studied by Bartholinus, who gave them the name of lymphatics.

The idea, which dates from the discoveries of Asellius and Pecquet, that the lacteals absorb all the products of digestion, was disproven by the experiments of Magendie and of those who experimented after him upon vascular absorption. It is now known that fats in the form of a very fine emulsion are absorbed by the lacteals, and that these are the only constituents of food taken up in great quantity by this system of vessels. It becomes an important question to determine, however, whether the lacteals be not concerned, to some extent, in the absorption of drinks, the albuminoids, saline and saccharine matters, etc. This question will be taken up after a consideration of certain points in the anatomy of the lymphatic system.

*Physiological Anatomy of the Lacteal and Lymphatic Vessels.*—The lacteals are the intestinal lymphatics; and during the intervals of intestinal absorption they carry a liquid which is identical with the contents of other lymphatic vessels. In their structure, also, the lacteals are identical with the general lymphatics.

Owing to the exceeding tenuity of the walls of the small lymphatics and the existence of great numbers of valves which prevent injection from the large trunks, the anatomy of these vessels is studied with some difficulty; and still greater difficulty is presented in the study of the vessels of origin of the lymphatic system in different tissues and organs. The origin of the lymphatics in the intestinal villi has already been considered, and it remains to study the origin of these vessels in other parts.

Comparatively recent investigations, particularly those of Von Recklinghausen and his followers, have entirely changed the views of anatomists with regard to the mode of origin of the lymphatics of various parts; but the results of these investigations are so definite and positive and have been so fully confirmed, that they are now almost universally adopted. According to these results, the lymphatics have several modes of origin.

In the connective tissues, which are so widely distributed in the body, there are always found, irregularly shaped, stellate spaces, which communicate

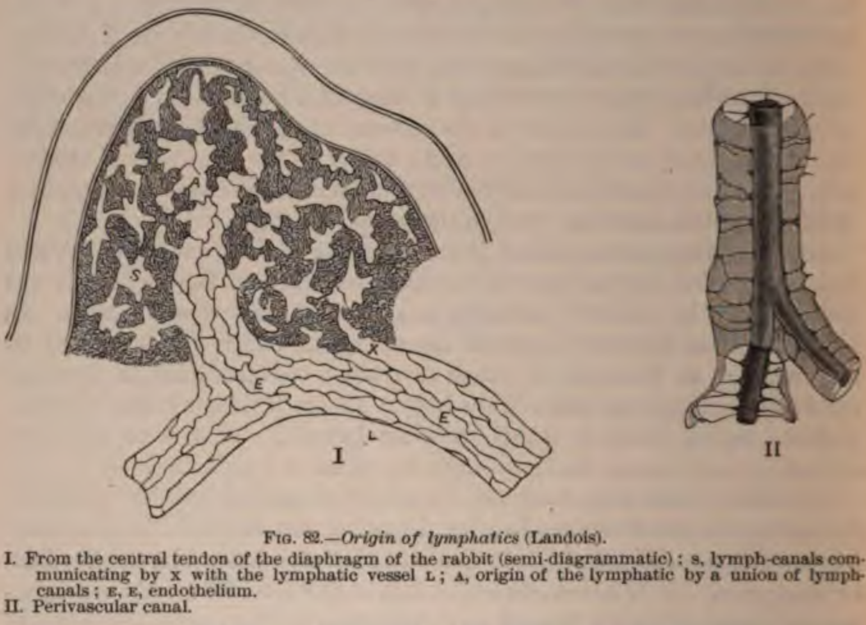


Fig. 82.—*Origin of lymphatics* (Landois).

I. From the central tendon of the diaphragm of the rabbit (semi-diagrammatic): S, lymph-canals communicating by X with the lymphatic vessel L; A, origin of the lymphatic by a union of lymph-canals; E, E, endothelium.
II. Perivascular canal.

with each other by branching canals, that can properly be called lymph-spaces, or "juice-canals." These spaces contain a liquid and large numbers of leucocytes. The leucocytes in these spaces may be called lymph-corpuscles, as they eventually find their way into the true lymphatic vessels; but they are thought to be white blood-corpuscles which have passed through the stomata of the capillary blood-vessels. The connective-tissue lymph-spaces, by certain of their branches, finally communicate with the so-called lymph-capillaries, through what have been regarded as the stomata of these vessels. These anatomical *data* have led to the following view with regard to the relations between the blood, the lymph and the tissues.

Nutrient matters are supplied to the parts by transudation through the walls of the capillary blood-vessels; and the effete matters pass from the lymph-spaces into the true lymphatic vessels, to be finally carried to the venous system. In certain tissues and organs, however, such as the cornea and fibrous membranes, the lymph-spaces or canals supply the nutrient fluid; and in the glands they probably supply part of the material used in the formation of the secretions.

In the serous membranes and in other analogous structures, there are large numbers of openings into the cavities; and the peritoneum, pleura, pericardium, tunica vaginalis testis, chambers of the eye, labyrinth of the internal ear and subarachnoid space are to be regarded as great lymph-sacs, the contained fluids being lymph, without, however, presenting the so-called lymph-corpuscles.

The relations between the blood-vessels and the smallest lymphatics are very close in certain parts. In the cerebro-spinal centres, Robin and His have demonstrated a system of canals which surround the small blood-vessels and are connected with the lymphatic-trunks or reservoirs described by Fohmann and found under the pia mater. The capillary blood-vessels thus float in surrounding vessels filled with liquid. These vessels surrounding the blood-vessels are called perivascular canals, and the contained liquid is true lymph, containing leucocytes, or lymph-corpuscles. They exceed the blood-vessels in diameter by $\frac{1}{1250}$ to $\frac{1}{400}$ of an inch (20 to 62$\mu$). Since the perivascular canals of the nerve-centres have been described, similar vessels have been found in the retina and in the liver.

The true capillary lymphatics have been studied in various parts by means of mercurial injections, but the presence of valves in the small trunks renders it necessary to make these injections from the periphery. The vessels have been injected in certain situations with mercury, by simply puncturing with a fine-pointed canula the parts in which the plexus is supposed to exist, and allowing the liquid to gently diffuse itself. Following the course of the vessels, the injection passes into the larger trunks and thence to the lymphatic glands. The regularity of the plexus through which the liquid is first diffused and the passage of the injection through the larger vessels to the glands are proof that the lymphatics have been penetrated and that the appearances observed are not the result of mere infiltration in the tissue. It does not appear that the vessels composing this plexus vary much in size. They are quite elastic, and after distention by injection, they return to a very small diameter when the fluid is allowed to escape.

By the method above indicated, it is possible to inject the superficial lymphatics of the skin, the deeper vessels situated just beneath the skin, and vessels in the serous membranes, glandular organs, lungs, tendons etc., in addition to the larger trunks, such as the thoracic duct. The lacteal system presents essentially the same anatomical characters as the general lymphatics, and the vessels are filled with colorless lymph during the intervals of digestion. In many situations the lymphatics present in their course little, solid structures, called lymphatic glands, although, as regards structure and office, they are not true glandular organs. The smallest capillary lymphatics have a diameter of about $\frac{1}{300}$ of an inch (83 $\mu$). This may be taken as their average diameter in the primitive plexus. This plexus, when the vessels are abundant, as they are in certain parts of the cutaneous surface, resembles an ordinary plexus of capillary blood-vessels, except that the walls of the vessels

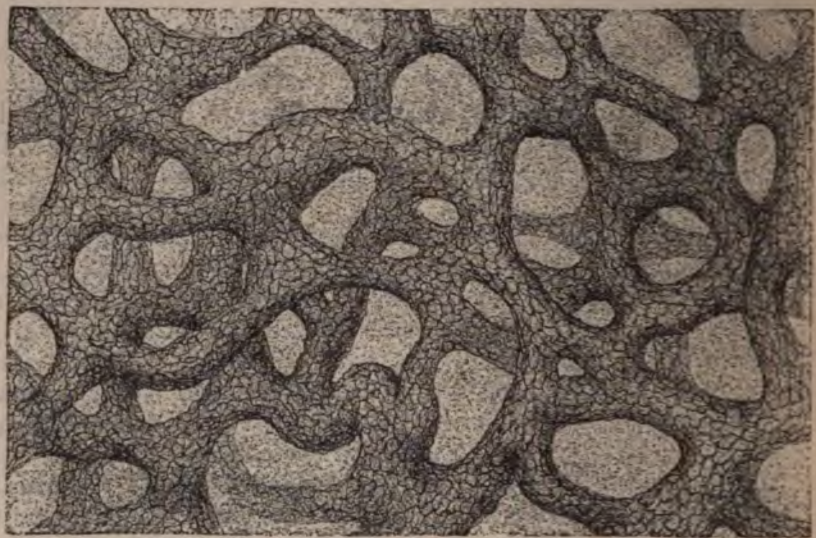

FIG. 83.—*Lymphatic plexus, showing the endothelium* (Belaieff).

are thinner and their diameter is greater. The vessels are lined by endothelial cells, the borders of which are brought into view by the action of silver nitrate, as is shown in Fig. 83.

The smallest lymphatic vessels are by far the most abundant. They are arranged in the form of a fine plexus, very superficially situated in the skin. A second plexus exists just beneath the skin, composed of vessels of much greater diameter. The skin is thus enclosed between two plexuses of capillary lymphatics. A plexus analogous to the superficial plexus of the skin is found just beneath the surface of the mucous membranes. These may, indeed, be classed with the superficial lymphatics. The deep lymphatics are much larger and less abundant, and their origin is less easily made out. These accompany the deeper veins in their course. They receive the lymph from the superficial vessels.

No valvular arrangement is found in the smallest lymphatics; but the vessels coming from the primitive plexuses, as well as the large vessels, contain valves in great numbers. These valves, being so closely set in the vessels, give to them, when filled with injection, a peculiar and characteristic beaded appearance.

The course of the lymphatics is generally direct. As they pass toward the great trunks by which they communicate with the venous system, they

FIG. 84.—*Superficial lymphatics of the skin of the palmar surface of the finger* (Sappey).


FIG. 85.—*Deep lymphatics of the skin of the finger* (Sappey).
1, 1, deep net-work of cutaneous lymphatics; 2, 2, 2, 2, lymphatic trunks connected with this net-work.

FIG. 86.—*Same finger, lateral view, showing lymphatic trunks connected with the superficial net-work* (Sappey).

present a peculiar anastomosis with the adjacent vessels, called anastomosis by bifurcation; that is, as a vessel passes along with other vessels nearly parallel with it, it bifurcates, and the two branches pass into the nearest vessels on either side. These anastomoses are quite frequent, and they generally occur between vessels of equal size. In their course, the vessels pass through the so-called lymphatic glands.

A notable peculiarity in the lymphatic vessels is that they vary very little in size, being nearly as large at the extremities as they are near the trunk. In their course, they are always much smaller than the veins and do not progressively enlarge as they pass on to the great lymphatic trunks. The largest vessels that pass from the skin are $\frac{1}{25}$ to $\frac{1}{12}$ of an inch (1 to 2 mm.) in diameter, and the larger vessels, in their course, have a diameter of $\frac{1}{12}$ to $\frac{1}{8}$ of an inch (2 to 3 mm.). As in the case of the smallest lymphatics of the primitive plexuses, the elasticity of the walls of the vessels renders their diameter greatly dependent upon the pressure of fluid in their interior. Many anatomists have noticed that vessels which are hardly perceptible while empty are capable of being dilated to the diameter of half a line (about 1 mm.)

or more, returning to their original size as soon as the distending fluid is removed.

In the lymphatics of the skin, the only important peculiarity which has not yet been mentioned is that the vessels appear to be very unequally distributed in different parts of the surface. According to Sappey, they are particularly abundant in the scalp over the biparietal suture, the soles of the feet and the palms of the hand, the fingers at the lateral portion of the last phalanges, and the scrotum. In the median portion of the scrotum they attain their highest degree of development. They are also found, though in less number, originating from around the median line on the anterior and posterior surface of the trunk, the posterior median portion of the extremities, the skin over the mammæ, and around the orifices of the mucous passages. Sappey has injected lymphatic vessels in the anterior portion of the forearm, the thigh and the leg, and in the middle portion of the face, although they are demonstrated with difficulty in these situations. If they exist at all in other portions of the cutaneous surface, they are not abundant.

FIG. 87.—*Superficial lymphatics of the arm* (Sappey).

FIG. 88.—*Superficial lymphatics of the leg* (Sappey).

In the mucous membranes the lymphatics are very abundant. Here are found, as in the skin, two distinct layers which enclose between them the entire thickness of the mucous membrane. The more superficial of these layers is composed of a rich plexus of small vessels, and beneath the mucous membrane, is a plexus consisting of vessels of larger size. The superficial plexus is very rich in the mixed structure which forms the lips and the glans penis, and around the orifices of the mouth, the nares, the vagina and the anus. There are certain mucous membranes in which the lymphatics have never been injected. In the serous membranes, lymphatics have been demonstrated in great abundance. Lymphatics have been demonstrated taking their origin in the voluntary muscles, the diaphragm, the heart and the non-striated muscular coats of the hollow viscera, although their investigation in these situations is difficult.

Lymphatics are found coming from the lungs in great numbers. These arise in the walls of the air-cells and surround each pulmonary lobule with a close plexus. The deep vessels follow the course of the bronchial tubes, passing through the bronchial glands and the glands at the bifurcation of the trachea, to empty into the thoracic duct and the great lymphatic duct of the right side.

In the glandular system, including the ductless glands, and in the ovaries, the lymphatic vessels are, as a rule, more abundant than in any other parts of the body. They are especially abundant in the testicles, the ovaries, the liver and the kidneys.

The lymphatic vessels from the superficial and deep portions of the head and face on the right side, and those from the superficial and deep portions of the right arm, the right half of the chest, and the mammary gland, with a few vessels from the lungs, pass into the great lymphatic duct, ductus lymphaticus dexter, which empties into the venous system at the junction of the right subclavian with the internal jugular. This vessel is about an inch (25·4 mm.) in length and one-twelfth to one-eighth of an inch (2 to 3 mm.) in diameter. It is provided with a pair of semilunar valves at its opening into the veins, which effectually prevent the ingress of blood. The vessels from the inferior extremities, and those from the lower portions of the trunk, the pelvic viscera, the abdominal organs generally and the left half of the body above the abdomen empty into the thoracic duct.

In their course, all of the lymphatics pass through the small, flattened, oval bodies, called the lymphatic glands, which are so abundant in the groin, the axilla, the pelvis and in some other parts. Two to six vessels, called the vasa afferentia, penetrate each gland, having first broken up into a number of smaller vessels just before they enter. They pass out by a number of small vessels which unite to form one, two or three trunks, generally of larger size than the vasa afferentia. The vessels which thus emerge from the glands are called vasa efferentia.

The lymphatics of the small intestine, called lacteals, pass from the intestine between the folds of the mesentery to empty, sometimes by one and sometimes by four or five trunks, into the receptaculum chyli. In their course, the lacteals pass through several sets of lymphatic glands, which are here called mesenteric glands.

The thoracic duct, into which most of the lymphatic vessels empty, is a vessel with very delicate walls and about the size of a goose-quill. It begins by a dilatation, more or less marked, called the receptaculum chyli. This is situated upon the second lumbar vertebra. The canal passes upward in the median line for the inferior half of its length. It then inclines to the left side, forms a semicircular curve something like the arch of the aorta, and empties at the junction of the left subclavian with the internal jugular vein.

It diminishes in size from the receptaculum to its middle portion and becomes larger again near its termination. It occasionally bifurcates near the middle of the thorax, but the branches become reunited a short distance above. At its opening into the venous system, there is generally a valvular fold, but according to Sappey, this is not constant. There is always, however, a pair of semilunar valves in the duct, three-quarters of an inch to an

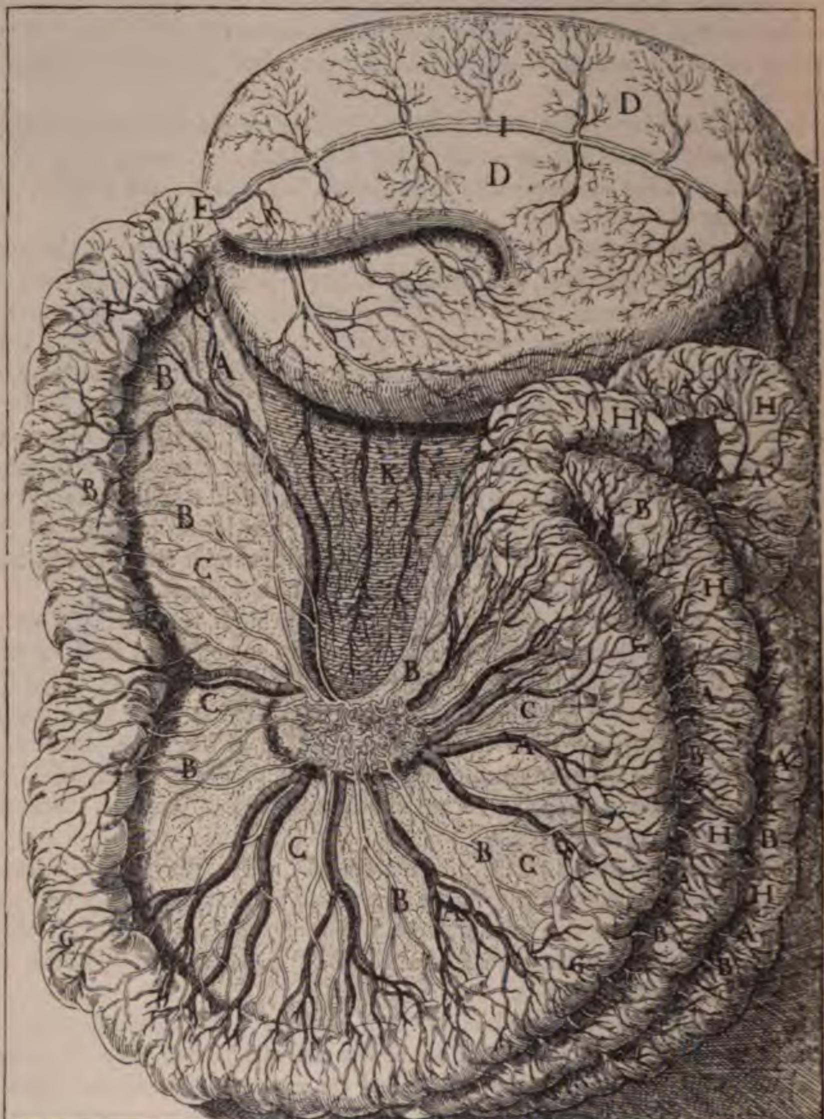

FIG. 89.—*Stomach, intestine and mesentery, with the mesenteric blood-vessels and lacteals* (copied and slightly reduced from a figure in the original work of Asellius, published in 1628).

A, A, A, A, A, mesenteric arteries and veins; B, B, B, B, B, B, B, B, B, B, lacteals; C, C, C, C, mesentery; D, D, stomach; E, pyloric portion of the stomach; F, duodenum; G, G, G, jejunum; H, H, H, H, H, ileum; I, artery and vein on the fundus of the stomach; K, portion of the omentum.

inch (19 to 25 mm.) from its termination, which effectually prevent the entrance of blood from the venous system.

The foregoing sketch of the descriptive anatomy of what has been called the absorbent system of vessels shows that they may collect fluids, not only from the intestinal canal during digestion, but from nearly every tissue and organ in the body, and that these fluids are finally received into the venous circulation.

*Structure of the Lacteal and Lymphatic Vessels.*—The lymphatic vessels, even those of largest size, are remarkable for the delicacy and transparency of their walls. This is well illustrated in the case of the lacteals, which are hardly visible in the transparent mesentery, unless they be filled with the opaque chyle.

From the difficulty in studying the lymphatics at their origin, except by means of injections or by reagents which stain the vessels, investigations into the structure of the smallest vessels have not been very satisfactory. It is supposed, however, that the vessels here consist of a single coat, resembling, in this regard, the capillary blood-vessels. Belaieff has described in the capillary lymphatics of the penis a lining of endothelial cells arranged in a single layer. These cells are oval, polygonal, fusiform or dentated, with their long diameter in the direction of the axis of the vessels.

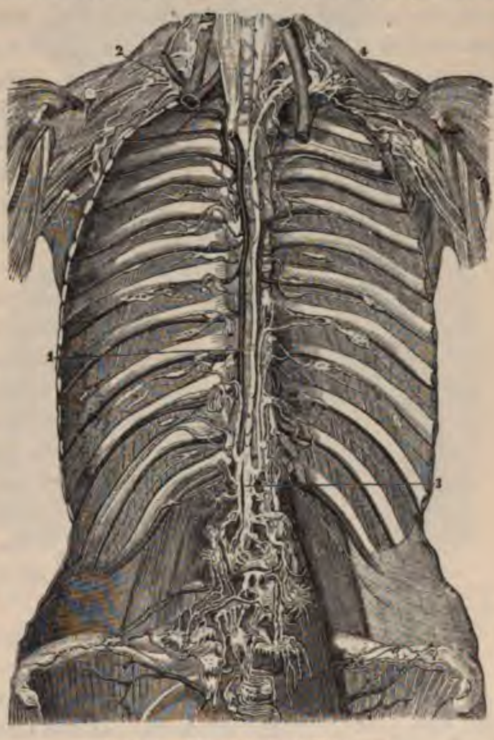


FIG. 90.—*Thoracic duct* (Mascagni).
1, thoracic duct; 2, great lymphatic duct; 3, receptaculum chyli; 4, curve of the thoracic duct just before it empties into the venous system.

In all but the capillary lymphatics, although the walls are very thin, three distinct coats can be distinguished. The internal coat consists of an elastic membrane lined with oblong, endothelial cells. This coat readily gives way when the vessels are forcibly distended. The middle coat is composed of longitudinal fibres of connective tissue, with delicate elastic fibres, and non-striated muscular fibres arranged transversely. The external coat is composed of the same structures as the middle coat, but most of the fibres are arranged longitudinally. In this coat the muscular fibres do not form a continuous sheet, but are collected into separate fasciculi, which have a direction either longitudinal or oblique. The fibres of connective tissue are very abundant and unite the vessels to the surrounding parts. The internal and the middle coats are closely adherent to each other; but the external coat may readily be separated from the others. Blood-vessels have been found in the walls of the lymphatics, and the existence of vaso-motor nerves is probable.

The walls of the lymphatic vessels are very closely adherent to the surrounding tissues; so closely, indeed, that even a small portion of a vessel is detached with great difficulty, and the vessels, even those of large size, can not be followed out and isolated for any considerable distance.

In all the lymphatic vessels, beginning a short distance from their plexus of origin, are semilunar valves, generally arranged in pairs, with their concavities looking toward the larger trunks. These folds are formed of the middle and inner coats; but the fold formed from the lining membrane is by far the wider, so that the free edges of the valves are considerably thinner than that portion which is attached directly to the vessel. The valves are most abundant in the superficial vessels. The distance between the valves is one-twelfth to one-eighth of an inch (2 to 3 mm.), near the origin of the vessels, and one-quarter to one-third of an inch (6 to 8 mm.), in their course. In the lymphatics situated between the muscles the valves are less abundant. They are always relatively few in the vessels of the head and neck and in all that have a direction from above downward. Although there are a number of valves in the thoracic duct, they are not so abundant here as in the smaller vessels.

FIG. 91.—*Valves of the lymphatics* (Sappey).

In their anatomy and general properties, the lymphatics bear a close resemblance to the veins. Although much thinner and more transparent, their coats have nearly the same arrangement. The arrangement of valves is entirely the same; and in both systems, the folds prevent the reflux of fluids when the vessels are subjected to pressure.

The lymphatics are very elastic; and it is generally admitted that the larger vessels and those of medium size are contractile, although the action of their muscular fibres, like that of all fibres of the non-striated variety, is slow and gradual.

One of the most important points in connection with the physiological anatomy of the lymphatic vessels is the question of the existence of orifices in their walls, which might allow the passage of solid particles or of emulsions. Anatomical observations have indicated the existence of stomata, of variable size and irregular shape, in the smallest vessels; and a strong argument in favor of the existence of these orifices has been the fact of the actual passage, through the walls of the vessels, of fatty particles, the entrance of which can not be explained by the well known laws of endosmosis. The anatomical evidence of the existence of openings is derived mainly from preparations stained with silver nitrate. It is assumed that silver nitrate stains the solid parts of tissues and the borders of the endothelial cells, and that non-nucleated areas which do not present any staining are necessarily open. In preparations of the lymphatics, the solution of silver is seen staining the tissues and the borders of the cells lining the vessels; but there are areas between these cells where no staining is observed and in which no nuclei are brought out by staining with carmine.

*Lymphatic Glands.*—In the course of the lymphatic vessels, are small, lenticular bodies, called lymphatic glands. The number of these is very great, although it is estimated with difficulty, from the fact that many of them are very small and are consequently liable to escape observation. It may be stated as an approximation that there are six or seven hundred lymphatic glands in the body. Their size and form are also very variable within the limits of health. They generally are flattened and lenticular, some as large as a bean and others as small as a small pea or even a pin's-head. They are arranged in two sets; one superficial and corresponding with the superficial lymphatic vessels, and a deep set, corresponding with the deep vessels. The superficial glands are most abundant in the folds at the flexures of the great joints and about the great vessels of the head and neck. The deep-seated glands are most abundant around the vessels coming from the great glandular viscera. A distinct set of large glands is found connected with the lymphatic vessels between the folds of the mesentery. These are known as the mesenteric glands. All of the lymphatic vessels pass through glands before they empty into the great lymphatic trunks, and most of them pass through several glands in their course.


FIG. 92.—*Lymphatics and lymphatic glands* (Sappey).
1, upper extremity of the thoracic duct, passing behind the internal jugular vein; 2, opening of the thoracic duct into the internal jugular and left subclavian vein. The lymphatic glands are seen in the course of the vessels.

The perfect, healthy glands are of a grayish-white or reddish color, of about the consistence of the liver, presenting a hilum where the larger blood-vessels enter and the efferent vessels emerge, and are covered, except at the hilum, with a delicate membrane composed of inelastic fibres, a few elastic fibres and non-striated muscular fibres. Their exterior is somewhat tuberculated, from the projections of the follicles just beneath the investing membrane. The interior of the glands is soft and pulpy. It presents a coarsely granular, cortical substance, of a reddish-white or gray color, which is one-sixth to one-fourth of an inch (4 to 6 mm.) in thickness in the largest glands. The medullary portion, which comes to the surface at the hilum, is lighter colored and coarser than the cortical substance. Throughout the gland, are found delicate fasciculi of fibrous tissue connected with the investing membrane, which serve as a fibrous skeleton for the gland and divide its substance into little alveoli. The structure is far more delicate in the cortical than in the medullary portion.

Within the alveoli, are irregularly oval, closed follicles, about $\frac{1}{250}$ of an inch (100 $\mu$.) in diameter, filled with a fluid and with cells like those contained in the solitary glands of the intestines and the patches of Peyer. These follicles do not seem to occupy the medullary portion of the glands, which, according to Kölliker, is composed chiefly of a net-work of lymphatic capillaries, mixed with rather coarse bands of fibrous tissue. The follicular structures in the lymphatic glands resemble the closed follicles in the mucous membrane of the intestinal canal and the Malpighian bodies of the spleen.

According to Von Recklinghausen, there exist in the substance of the lymphatic glands great numbers of lymph-spaces or canals, which are probably lined with endothelium; and these spaces communicate with the efferent vessels, by the stomata. The afferent vessels, two to six in number, penetrate the gland, and probably empty their contents into the lymph-spaces. The lymph is then collected from the lymph-spaces, by the vasa efferentia, one to three in number, which are always larger than the afferent vessels.

Fig. 93.—*Different varieties of lymphatic glands* (Sappey).

The lymphatic glands are supplied with blood, sometimes by one but generally by several small arteries, which penetrate at the hilum. These vessels pass directly to the medullary portion and there break up into several coarse branches to be distributed to the cortical substance, where they ramify in a delicate, capillary net-work with rather wide meshes, in the closed follicles found in this portion of the gland. This capillary plexus also receives branches from small arterial twigs which penetrate the capsule of the gland at different points. Returning on themselves in loops, the vessels unite to form one or more large veins, which generally emerge at the hilum.

Very little is known regarding the distribution of nerves in the lymphatic glands. A few filaments from the sympathetic system enter with the arteries, but they have never been traced to their final distribution. The entrance of filaments from the cerebro-spinal system has never been demonstrated.

It is evident, from the structure of the lymphatic glands, that they must materially retard the passage of the lymph toward the great trunks; and it is well known in pathology that morbid matters taken up by the absorbents are frequently arrested and retained in the nearest glands.

The uses of the lymphatic glands are somewhat obscure. They are supposed, however, to have an important office in the elaboration of the corpuscular elements of the lymph and chyle; and it has been observed that the lymph contained in vessels which have passed through no glands is relatively poor in corpuscles, while the large trunks and the efferent vessels contain them in large numbers.

*Absorption of Albuminoids by the Lacteals.*—Comparative analyses of the lymph and chyle always show in the latter fluid an excess of albuminoid matters; and it is natural to infer that the excess of nitrogenized matters in the chyle is due to absorption of albuminoids from the intestinal canal. Lane collected the chyle from the lacteals of a donkey, seven and a half hours after a full meal of oats and beans, and compared its composition with that of the lymph. The analyses were made by Rees, who found that the chyle contained about three times as much albumen and fibrin as the lymph. While by far the greatest part of the products of digestion of the albuminoids is absorbed by the blood-vessels, there can be no doubt that a small portion is also taken up by the lacteals.

*Absorption of Glucose and Salts by the Lacteals.*—What has just been stated regarding the absorption of albuminoids applies to saccharine matters and the inorganic salts. Small quantities of sugar and sometimes lactic acid have been detected in the chyle from the thoracic duct in the herbivora; and the presence of sugar in both the lymph and the chyle has been determined by Colin. While the products of the digestion of saccharine and amylaceous matters are taken up mainly by the blood-vessels, a small quantity is also absorbed by the lacteals. In the comparative analyses of the chyle and lymph by Rees, the proportion of inorganic salts was found to be considerably greater in the chyle. The great excess in the quantity of blood coming from the intestine, and the rapidity of its circulation, as compared with the chyle, will explain the more rapid penetration by endosmosis of the soluble products of digestion.

*Absorption of Water by the Lacteals.*—There can be no doubt that a small portion of the liquids taken as drink finds its way into the circulation by the lacteals, although the greatest part passes directly into the blood-vessels. This has been proved by experiments of a most positive character. When an animal has taken solid food only and is killed during digestion, the thoracic duct contains a very small quantity of chyle; but when the animal has taken liquids with the food, the thoracic duct and the lacteals are very much distended (Leuret and Lassaigne). In an experiment by Ernest Burdach, a dog was deprived of food and drink for twenty-four hours, after which he was allowed to drink water, and in addition, half a pound(227 c. c.) was injected into the stomach. The animal was killed a half-hour after, and the thoracic duct was found engorged with watery lymph, which contained a very few lymph-corpuscles.

Aside from the entrance of gases into the blood from the pulmonary surface, physiological absorption is almost entirely confined to the mucous membrane of the alimentary canal. It is true that liquids may find their way into the circulation through the skin, the lining membrane of the air-passages, the reservoirs, ducts and parenchyma of glands, the serous and other closed cavities, the areolar tissue, the conjunctiva, the muscular tissue, and, in fact, all parts which are supplied with blood-vessels; but here the absorption of foreign matters is occasional or accidental and is not connected with the general process of nutrition. It is now well known that all parts of the body, except the epidermis and its appendages, the epithelium, and some other structures which are regularly desquamated, are constantly undergoing change, and the effete matters which result from their disassimilation are taken up by what is called interstitial absorption, and are carried by the blood to the proper organs, to be excreted. It seems probable that the vessels of these parts would also be capable of absorbing soluble foreign substances; and this is, indeed, the fact with regard to all parts in which the nutritive processes are even moderately active or where the structures covering the vascular parts are permeable.

*Absorption by the Skin.*—It is universally admitted that absorption can take place from the general surface, although at one time this was a question much discussed by physiologists. The proofs, however, of the entrance of certain medicinal preparations from the surface of the body are now entirely conclusive; and the constitutional effects of medicines administered in this way are frequently as marked as when they are taken into the alimentary canal. The question which is of most importance in this connection relates to the normal action of the skin as an absorbing surface. Looking at this subject from a purely physiological point of view, absorption from the skin, under ordinary conditions, must be very slight, if, indeed, it take place at all. There are, nevertheless, facts which render it certain that water may be absorbed by the skin. In a series of experiments by Collard de Martigny, in 1821, it was shown that water could be absorbed in small quantity by the skin of the palm of the hand. In one experiment, a small bell-glass filled with water was applied hermetically to the palm. This was connected with a tube bent in the form of a siphon, also filled with water, the long branch of which was placed in a vessel of mercury. After the apparatus had been applied for an hour and three-quarters, the mercury was found sensibly elevated in the tube, showing that a certain quantity of the water had disappeared. In a series of observations upon the absorption of water and soluble substances, by Willemin (1863), it was shown that water is absorbed in a bath, and that various medicinal substances may be taken up by the skin in this way and can be detected afterward in the urine.

It has been frequently remarked that the sensation of thirst is always least pressing in a moist atmosphere, and that it may be allayed to a certain extent by baths. It is true that in a moist atmosphere the cutaneous exhalations are diminished, and this might account for the maintenance of the normal proportion of fluids in the body with a less amount of drink than ordinary; but one could hardly account for an actual alleviation of thirst by immersion of the body in water, unless it were assumed that a certain quantity of water had been absorbed. A striking example of relief of thirst in this way is given by Captain Kennedy, in the narrative of his sufferings after shipwreck, when he and his men were exposed for a long time without water, in an open boat. With regard to his sufferings from thirst, he says: "I can not conclude without making mention of the great advantage I derived from soaking my clothes twice a day in salt-water, and putting them on without wringing. . . . There is one very remarkable circumstance, and worthy of notice, which was, that we daily made the same quantity of urine as if we had drunk moderately of any liquid, which must be owing to a body of water absorbed through the pores of the skin. . . . So very great advantage did we derive from this practice, that the violent drought went off, the parched tongue was cured in a few minutes after bathing and washing our clothes; at the same time we found ourselves as much refreshed as if we had received some actual nourishment."

*Absorption by the Respiratory Surface.*—Animal and vegetable emanations may be taken into the blood by the lungs and produce certain well marked pathological conditions. Many contagious diseases are propagated in this way, as well as some fevers and other general diseases which are not contagious. With regard to certain poisonous gases and volatile matters, the effects of their absorption by the lungs are even more striking. Carbon monoxide and arsenious hydride produce death almost instantly, even when inhaled in small quantity. The vapor of pure hydrocyanic acid acts frequently with great promptness through the lungs. Turpentine, iodine and many medicinal substances may be introduced with great rapidity by inhalation of their vapors; and the serious effects produced by the emanations from lead or mercury, in persons who work in these articles, are well known. Not only have vapors introduced in this way been recognized in the blood, but many of the matters thus absorbed are excreted by the kidneys and may be detected by their characteristic reactions in the urine.

As would naturally be expected, water and substances in solution, when injected into the respiratory passages, are rapidly absorbed, and poisons administered in this way manifest their peculiar effects with great promptness. Experimenters on this subject have shown the facility with which liquids may be absorbed from the lungs and the air-passages, but it must be remembered that the natural conditions are never such as to admit of this action. The normal office of the lungs is to absorb oxygen and sometimes a little nitrogen from the air; and the absorption of any thing else by these surfaces is unnatural and generally deleterious.

*Absorption from Closed Cavities, Reservoirs of Glands, etc.*—Facts in pathology, showing absorption from closed cavities, the areolar tissue, the muscular and nervous tissues, the conjunctiva and other parts, are sufficiently well known. In cases of effusion of serum into the pleural, peritoneal, pericardial or synovial cavities, in which recovery takes place, the liquid becomes absorbed. It has been shown by experiment that warm water injected into these cavities is disposed of in the same way. Effusions into the areolar tissue are generally removed by absorption. In cases of penetration of air into the pleura or the general areolar tissue, absorption likewise takes place; showing that gases may be taken up in this way as well as liquids. Effusions of blood beneath the skin or the conjunctiva or in the muscular or nervous tissue may become entirely or in part absorbed. It is true that these are pathological conditions, but in the closed cavities, the processes of exhalation and absorption are constantly going on, although not very actively. As regards absorption from the areolar tissue, the administration of remedies by the hypodermatic method is a familiar evidence of the facility with which soluble substances are taken into the blood, when introduced beneath the skin.

Under some conditions, absorption takes place from the reservoirs of the various glands, the watery portions of the secretions being generally taken up, leaving the solid and the organic matters. It is supposed that the bile becomes somewhat inspissated when it has remained for a time in the gall-bladder, even when the natural flow of the secretion is not interrupted. Certainly, when the duct is in any way obstructed, absorption of a portion of the bile takes place, as is shown by coloration of the conjunctiva and even of the general surface. The serum of the blood, under these conditions, is always strongly colored with bile. It is probable, also, that some of the watery portions of the urine are reabsorbed by the mucous membrane of the urinary bladder when the urine has been long confined in its cavity, although this reabsorption is ordinarily very slight. Absorption may take place from the ducts and the parenchyma of glands, although this occurs chiefly when foreign substances have been injected into these parts.

### Absorption of Fats and Insoluble Substances.

The general proposition that all substances capable of being absorbed are soluble in water or in the digestive fluids must be modified in the case of the fats. These are never dissolved in any considerable quantity in digestion, the only change which they undergo being a minute subdivision in the form of a very fine emulsion. In this condition the fats are taken up by the lacteals and may be absorbed in small quantity by the blood-vessels.

In studying the mechanism of the penetration of fatty particles into the intestinal villi, it has been ascertained that the epithelial cells covering the villi play an important part in this process. During the digestion of fat, these cells become filled with fatty granules (Goodsir). Funke, in his atlas of physiological chemistry, figures the appearances of the intestinal epithelium during the digestion of fat, as contrasted with the epithelium observed during the intervals of digestion, showing the cells, during absorption, filled with fatty granules.

It has not been demonstrated exactly how the fatty particles penetrate the epithelium of the villi, but the fact of such penetration is undoubted. From the epithelium, the particles of emulsion pass into the substance of the villi—probably into the lymph-spaces and canals—and from these they readily find their way into the lymphatic capillaries. It has been shown that fatty emulsion will pass more easily through porous *septa* that have been moistened with bile; and it is probably in this way mainly that the bile aids in the passage of the fine particles of fat into the lacteals.

FIG. 94.—*Epithelium of the small intestine of the rabbit* (Funke).

As a general law, insoluble substances, with the exception of the fats, are never regularly absorbed, no matter how finely they may be divided. The apparent exceptions to this are mercury in a state of minute subdivision like an emulsion, and carbonaceous particles. As regards mercury, it is well known that minute particles in the form of unguents may be introduced into the system by prolonged frictions; but this can not be taken as an instance of physiological absorption. The passage of small, carbonaceous particles through the pulmonary membrane seems to be purely mechanical. The same thing may possibly occur when fine, sharp particles of carbon are introduced

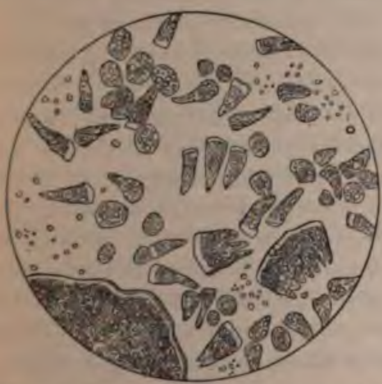

FIG. 95.—*Epithelium from the duodenum of a rabbit, two hours after having been fed with melted butter* (Funke).

FIG. 96.—*Villi filled with fat, from the small intestine of an executed criminal, one hour after death* (Funke).

into the alimentary canal; but the experiments of Mialhe with pulverized charcoal, and particularly those of Bérard, Robin and Bernard with lamp-black introduced into the intestinal canal of animals, showed that although the intestinal mucous membrane became of a deep black, this could easily be removed by a stream of water and no carbonaceous particles could be discovered in the mesenteric veins, the lacteals or the mesenteric glands. When the carbon is used in the form of lamp-black, the particles are very minute and rounded, and they do not present the sharp points and edges which sometimes enable the grains of pulverized charcoal to penetrate the vessels mechanically.

### Variations and Modifications of Absorption.

Very little is known concerning the variations in lacteal or lymphatic absorption; but in absorption by blood-vessels, important modifications occur, due, on the one hand, to different conditions of the fluids to be absorbed, and on the other, to differences in the constitution of the blood and in the conditions of the vessels.

The different conditions of the fluids to be absorbed apparently do not always have the same influence in physiological absorption as in endosmotic experiments made out of the body. Saccharine solutions of different densities confined in distinct portions of the intestinal canal of a living animal do not present any marked variations in the rapidity of their absorption, and they are taken up by the blood, even when their density is greater than that of the blood-plasma. Solutions of potassium nitrate and of sodium sulphate, of greater density than the serum, which would, therefore, attract the endosmotic current in an endosmometer, are readily taken up by the blood-vessels in a living animal. Indeed, nearly all soluble substances, whatever be the density of their solutions, may be taken up by the various absorbing surfaces during life. The curare poison and most of the venoms are remarkable exceptions to this rule. In a series of experiments upon the absorption of curare, Bernard has shown that this poison, which is absorbed so readily from wounds or when injected under the skin, generally produces no effect when introduced into the stomach, the small intestine or the urinary bladder. This result, however, is not invariable, for poisonous effects are produced when curare is introduced into the stomach of a fasting animal. This peculiarity in the absorption of many of the animal poisons has long been observed; and it is well known that the flesh of animals poisoned with curare may be eaten with impunity. It is curious, however, to see an animal carrying in the stomach without danger a fluid which would produce death if introduced under the skin; and the explanation of this is not readily apparent. The poison is not neutralized by the digestive fluids, for curare digested for a long time in gastric juice, or taken from the stomach of a dog, is found to possess all its toxic properties. This may be shown by poisoning a pigeon with curare drawn by a fistula from the stomach of a living dog (Bernard). If the absorption of this poison be recognized simply by its effects upon the system, it must be assumed that during digestion, it can not be absorbed by the mucous membrane of the stomach and small intestine, notwithstanding its solubility.

It has been shown that liquids which immediately disorganize the tissues, such as concentrated nitric or sulphuric acid, can not be absorbed. Another important peculiarity in absorption is that solutions which readily coagulate the albumen of the circulating fluids are absorbed very slowly (Miahle). This is explained by the supposition that there is a coagulation of the albuminous fluids with which the absorbing membrane is permeated, which interferes with the passage of liquids. These substancs are nevertheless taken up by the blood-vessels, though rather slowly.

*Influence of the Condition of the Blood and of the Vessels on Absorption.*—After loss of blood or deterioration of the nutritive fluid from prolonged abstinence, absorption generally takes place with great activity. This is well known, both as regards the entrance of water and alimentary substances and the absorption of medicines. It was at one time quite a common practice to bleed before administering certain remedies, in order to produce their more speedy action upon the system.

The rapidity of the circulation has an important influence in facilitating absorption, and this process is generally active in proportion to the vascularity of different parts. During intestinal absorption, the increase in the activity of the circulation in the mucous membrane is very marked and undoubtedly has an influence upon the rapidity with which the products of digestion are taken up by the blood.

*Influence of the Nervous System on Absorption.*—It is certain that absorption, especially in the stomach, is subject to certain variations, which can hardly be dependent upon anything but nervous action. Water and other liquids, which usually are readily absorbed from the stomach, are sometimes retained for a time, and are afterward rejected in nearly the condition in which they were taken. It is probable, however, that the most important influences thus exerted by the nervous system are effected through the circulation. The experiments of Bernard and others upon the vaso-motor nerves, by the action of which the supply of blood in different parts is regulated, point out a line of experimentation which would probably throw much light upon some of the important variations in absorption. When it is remembered that the small arteries may become so contracted under the influence of the vaso-motor nerves that their caliber is almost obliterated, of course retarding in a corresponding degree the capillary and venous circulation in the parts, and again, that the same vessels may be so dilated as to admit to a particular part many times more blood than it ordinarily receives, it becomes apparent that absorption may be profoundly affected through this system of nerves. It has been ascertained that while a section of some of the nerves distributed to the alimentary canal will slightly retard the absorption of the poisonous substances, the process is never entirely arrested.

### Imbibition and Endosmosis.

If liquids pass through the substance of an animal membrane, it is evident that the membrane itself must be capable of taking up a certain portion by imbibition; and this must be considered as the starting-point in absorption.

Imbibition is, indeed, a property common to all animal tissues. It is a well known fact, however, that the tissues do not imbibe all solutions with the same degree of activity. Distilled water is the liquid which is always taken up in greatest quantity, and saline solutions enter the substance of the tissues in an inverse ratio to their density. This is also the fact with regard to mixtures of alcohol and water, imbibition always being in an inverse proportion to the quantity of alcohol present in the liquid. Among the other conditions which have a marked influence upon imbibition, is temperature. It is a familiar fact that dried animal membranes may be more rapidly softened in warm than in cold water; and with regard to the imbibition of liquids by sand, the researches of Matteucci and Cima have shown a considerable increase at a moderately elevated temperature. While nearly all the structures of the body, after desiccation, will imbibe liquids, the membranes through which the processes of absorption are most active are, as a rule, most easily permeated; and the character of the liquid, the temperature etc., have a great influence upon the activity of this process. For example, all liquids which have a tendency to harden the tissues, such as saline solutions, alcohol etc., pass through with much less rapidity than pure water.

*Mechanism of the Passage of Liquids through Membranes.*—The passage of liquids through membranes is called osmosis. In the case of two liquids passing in opposite directions, the stronger current is called endosmotic and the weaker current is called exosmotic. In the passage of liquids into the vessels, in physiological absorption, the process is generally called endosmosis. The attention of physiologists was first directed to these phenomena by the researches of Dutrochet, published in 1826.

It is now definitely ascertained that the following conditions are necessary for the operation of endosmosis and exosmosis:

1. That both liquids be capable of "wetting" the interposed membrane, or in other words, that the membrane be capable of imbibing both liquids. If but one of the liquids can wet the membrane, the current takes place in only one direction.

2. That the liquids be miscible with each other and be differently constituted. Although it is found that the currents are most active when the liquids are of different densities, this condition is not indispensable; for currents will take place between solutions of different substances, such as salt, sugar or albumen, when they have precisely the same density.

The physiological applications of the laws of endosmosis can now be more fully appreciated, as it is evident that the above conditions are fulfilled whenever absorption takes place, with the single exception of the absorption of fats, which has been specially considered. For example, all substances are dissolved or liquefied before they are absorbed, and in this condition, they are capable of "wetting" the walls of the blood-vessels. All the liquids absorbed are capable, also, of mixing with the plasma of the blood. What makes this application still more complete, is the behavior of albumen in endosmotic experiments. In physiological absorption, there is always a great predominance of the endosmotic current, and there is very little transudation, or exosmosis, of the albuminoid constituents of the blood. On the other hand, there is a constant absorption of peptones, which are destined to be converted into the albuminoid constituents of the blood.

Recognizing the fact that albumen is capable of inducing a more powerful endosmotic current than almost any other liquid, it has been shown that it never itself passes through membranes in the exosmotic current, but that albuminoids, after transformation by digestion into peptones, or albumen mixed with gastric juice, pass through animal membranes with great facility. The experiments by which these facts are demonstrated are of the highest physiological importance. On removing part of the shell of an egg, so as to expose its membranes, and immersing it in pure water, the passage of water into the egg is rendered evident by the projection of the distended membranes; but although the surrounding liquid becomes alkaline and the appropriate tests reveal the presence of some of the inorganic constituents of the egg, the presence of albumen can not be detected. When the contents of the egg are replaced by the serum of the blood, the same result follows. "After six or eight hours of immersion, the serum had yielded to the water in the vessel all its saline elements, chlorides, sulphates, phosphates, which were easily recognized by their peculiar reactions, but not a trace of albumen" (Dutrochet).

A very simple apparatus for illustrating endosmotic action can be constructed in the following way: Remove carefully a circular portion, about an inch (25·4 mm.) in diameter, of the shell from one end of an egg, which may be done without injuring the membranes, by cracking the shell into small pieces, which are picked off with forceps. A small, glass tube is then introduced through an opening in the shell and membranes of the other end of the egg, and is secured in a vertical position by wax or plaster of Paris, the tube penetrating the yelk. The egg is then placed in a wine-glass partly filled with water. In the course of a few minutes the water will have penetrated the exposed membrane, and the yelk will rise in the tube.

Fig. 97.—*Egg prepared so as to illustrate endosmotic action.*

The force with which liquids pass through membranes, called endomostic or osmotic force, is to a great degree dependent upon the influence of the membranes themselves. This influence is always purely physical, in experiments made out of the body; and physiological absorption can be explained, to a certain extent, by the same laws. It must be remembered, however, that the properties of organic structures, which are manifested only in living bodies, are capable of modifying these physical phenomena in a remarkable degree. For example, all living tissues are capable of selecting and appropriating from the nutritive fluids the materials necessary for their regeneration; and the secreting structures of glands also select from the blood certain constitutents which are used in the formation of their secretions. These phenomena and their modifications through the nervous system can not be fully explained. This is true, also, of many of the phenomena of absorption and their modifications, which are probably dependent upon the same kind of action.

It is not necessary to assume the existence of infinitely small openings in homogeneous membranes through which osmotic currents can be made to take place, in order to explain the mechanism of these currents. In the case of two liquids capable of diffusing with each other and separated by an animal membrane, the mechanism of the endosmotic and exosmotic currents is very simple. In the first place, the membrane imbibes both the liquids, but one is always taken up in greater quantity than the other. If water and a solution of common salt be employed, the surface of the membrane exposed to the water will imbibe more than the surface exposed to the saline solution; but both liquids will meet in its substance. The first step, therefore, in the production of the currents is imbibition. Once in contact with each other, the liquids diffuse, the water passing to the saline solution, and *vice versâ*. This takes place by precisely the same mechanism as that of the passage of liquids through porous *septa*.

In no experiments performed out of the body, can the conditions favorable to the passage of liquids through membranes in accordance with purely physical laws be realized as they exist in the living organism. The great extent of the absorbing surfaces; the delicacy and permeability of the membranes; the rapidity with which substances are carried on by the torrent of the circulation, as soon as they pass through these membranes; the uniformity of the pressure, notwithstanding the penetration of liquids; all these favor the physical phenomena of absorption in a way which can not be imitated in artificially constructed apparatus. Within the blood-vessels, the albuminoid matters exist in a form which does not permit them to pass through membranes, while the peptones are highly osmotic. The sugars, also, pass through the walls of the vessels with facility, as well as various salts and medicinal substances in solution. The fats, as has been stated, pass mainly into the lacteals, by a process which has already been described and which can not be fully explained by the laws of endosmosis.

## Lymph and Chyle.

To complete the history of physiological absorption, it will be necessary to treat of the origin, composition and properties of the lymph and chyle. It is only within a few years that physiologists have been able to appreciate the importance of the lymph, for the experiments indicating the great quantity of this liquid which is continually passing into the blood are of comparatively recent date.

The first successful experiments in which the lymph and chyle were obtained in quantity were made by Colin. This observer, in operating upon large animals, particularly the ruminants, experienced no great difficulty in isolating the thoracic duct near its junction with the subclavian vein and introducing a metallic tube of sufficient size to allow the free discharge of fluid. These experiments, made upon horses and the larger ruminants, were the first to give any clear idea of the quantity of liquids—lymph and chyle—which pass through the thoracic duct. In an observation upon a cow of medium size, he succeeded in collecting, in the course of twelve hours, 105·3 lbs. (47,963 grammes); and he stated that a very much greater quantity can be obtained by operating upon ruminants of larger size.

According to the estimates of Dalton, deduced from his own observations upon dogs and the experiments of Colin upon horses, the total quantity of lymph and chyle produced in the twenty-four hours in a man weighing one hundred and forty-three pounds (65 kilos.) is about 6·6 pounds (3,000 grammes). And again, reasoning from experiments made upon dogs thirteen hours after feeding, when the fluid which passes up the thoracic duct may be assumed to be pure, unmixed lymph, the total quantity of lymph alone, produced in the twenty-four hours by a man of ordinary weight, would be about 4·4 pounds (2,000 grammes). These estimates can be accepted only as approximate, and they do not indicate the entire quantity of lymph actually contained in the organism.

There are no very satisfactory recent researches with regard to the physiological variations in the quantity of lymph. Collard de Martigny found the lymphatics always distended with fluid in dogs killed after two days of total deprivation of food. This condition continued during the first week of starvation; but after that time, the quantity in the vessels gradually diminished, and a few hours before death, the lymphatics and the thoracic duct were nearly empty. In comparing the quantity of fluid in the lymphatics of the neck, during digestion and absorption, with the quantity which they contained soon after digestion was completed, the same observer found that while digestion and absorption were going on actively, the vessels of the neck contained scarcely any fluid; but the quantity gradually increased after these processes were completed.

*Properties and Composition of Lymph.*—Lymph taken from the vessels in various parts of the system, or the fluid which is discharged from the thoracic duct during the intervals of digestion, is either perfectly transparent and colorless or of a slightly yellowish or greenish hue. When allowed to stand for a short time, it becomes faintly tinged with red, and frequently it has a pale rose-color when first discharged. Microscopical examination shows that this reddish color is dependent upon the presence of a few red blood-corpuscles, which are entangled in the clot as the lymph coagulates, thus accounting for the deepening of the color when the fluid has been allowed to stand.

Lymph has no decided or characteristic odor. It is very slightly saline in taste, being almost insipid. Its specific gravity is much lower than that of the blood. Magendie found the specific gravity in the dog to be about 1022. According to Robin, the specific gravity of the defibrinated serum of lymph is 1009. In analyses by Dähnhardt, of the lymph taken from dilated vessels in the leg, in the human subject, the specific gravity was 1007.

A few minutes after discharge from the vessels, both the lymph and chyle undergo coagulation. This process, as regards the chemical changes involved, is identical with the coagulation of the blood, in which the leucocytes play an important part. According to Colin, the fluid collected from the thoracic duct in the large ruminants coagulates at the end of five, ten or twelve minutes, and sets into a mass having exactly the form of the vessel in which it is contained. The clot is tolerably consistent, but there is never any spontaneous separation of serum (Colin). This may be the fact with regard to the lymph and the chyle of the large ruminants, but in the observations of Dalton, who operated upon dogs and goats, after a few hours' exposure, the clot contracted to about half its original size, precisely like coagulated blood, expressing a considerable quantity of serum. In one instance, in the dog, the volume of serum, after twenty-four hours of repose, was about twice that of the contracted clot.

Although many analyses have been made of lymph from the human subject, the conditions under which the fluid has been obtained render it probable that in the majority of instances it was not entirely normal. It will be necessary, therefore, to compare these analyses with observations made upon the lymph of the inferior animals; as in the latter, this fluid has been collected under conditions which leave no doubt as to its normal character. In the experiments of Colin especially, the fluids taken from the thoracic duct during the intervals of digestion undoubtedly represented the normal, mixed lymph collected from nearly all parts of the body; and the operative procedure in the large ruminants is so simple as to produce little if any general disturbance. The following is an analysis by Lassaigne of specimens of lymph collected by Colin from the thoracic duct of a cow, under the most favorable conditions:

COMPOSITION OF LYMPH FROM A COW.

| | |
|---|---|
| Water | 964·0 |
| Fibrin | 0·9 |
| Albumen | 28·0 |
| Fatty matter | 0·4 |
| Sodium chloride | 5·0 |
| Sodium carbonate, sodium phosphate and sodium sulphate | 1·2 |
| Calcium phosphate | 0·5 |
| | 1,000·0 |

The proportions given in the table are by no means invariable, the differences in coagulability indicating differences in the proportion of fibrin-factors, and the degree of lactescence showing great variations in the quantity of fatty matters. The table may be taken, however, as an approximation of the average composition of the lymph of these animals, during the intervals of digestion.

The analysis of human lymph which seems to be the most reliable, and in which the fluid was apparently pure and normal, is that of Gubler and Quevenne. The lymph in this case was collected by Desjardins from a female who suffered from a varicose dilatation of the lymphatic vessels in the anterior and superior portion of the left thigh. These vessels occasionally ruptured, and the lymph could then be obtained in considerable quantity.

When an opening existed, the discharge of fluid could be arrested at will by flexing the trunk upon the thigh. Gubler and Quevenne made analyses of two different specimens of the fluid, with the following results:

COMPOSITION OF HUMAN LYMPH.

| | First analysis. | Second analysis. |
|---|---|---|
| Water | 939·87 | 934·77 |
| Fibrin | 0·56 | 0·63 |
| Caseous matter (with earthy phosphates and traces of iron) | 42·75 | 42·80 |
| Fatty matter (in the second analysis, fusible at 102·3° Fahr., or 39° C) | 3·82 | 9·20 |
| Hydro-alcoholic extract (containing sugar, and leaving, after incineration, sodium chloride, with sodium phosphate and sodium carbonate) | 13·00 | 12·60 |
| | 1,000·00 | 1,000·00 |

The above analyses show a much larger proportion of solid constituents than was found by Lassaigne in the lymph of the cow. This excess is pretty uniformly distributed throughout all the constituents, with the exception of the fatty matters and fibrin; the former existing largely in excess in the human lymph, especially in the second analysis, while the latter is smaller in quantity than in the lymph of the cow. It is evident, however, from a comparison of the two analyses by Gubler and Quevenne, that the composition of the lymph, even when it is unmixed with chyle, is subject to great variations. The caseous matter given by Gubler and Quevenne is probably equivalent to the albuminous matter mentioned by other chemists.

The distinctive characters of the different constituents of the lymph do not demand extended consideration, inasmuch as most of them have already been treated of in connection with the blood. In comparing, however, the composition of the lymph with that of the blood, the great excess of solid constituents in the latter fluid is at once apparent.

In nearly all analyses the organic nitrogenized constituents have been found to be very much less in the lymph than in the blood. This is generally most marked with regard to the fibrin-factors; but as before stated, the proportion of all these substances is quite variable. On account of this deficiency, lymph is much inferior to the blood in coagulability, and the coagulum, when it is formed, is soft and friable. There does not appear, however, to be any actual difference between the coagulating constituents of the lymph and of the blood.

Fatty matters have generally been found to be more abundant in the lymph than in the blood; but their proportion is even more variable than that of the albuminoid constituents.

Very little remains to be said concerning the ordinary inorganic constituents of the lymph. The analyses of Dähnhardt have shown that nearly if not all of the inorganic matters which have been demonstrated in the blood are contained in the lymph; and a small proportion of iron is given in the analyses by Gubler and Quevenne.

These facts indicate a remarkable correspondence in composition between the lymph and the blood. All of the constituents of the blood, except the red corpuscles, exist in the lymph, the only difference being in their relative proportions.

In addition to the constituents of the lymph ordinarily given, the presence of glucose, and more lately, the existence of a certain proportion of urea, have been demonstrated in this fluid. It has not been ascertained how the sugar contained in the lymph takes its origin.

The presence of urea in considerable quantity in both the chyle and the lymph has been determined by Wurtz; and it is thought by Bernard that the lymph is the principal fluid, if not the only one, by which this excrementitious substance is taken up from the tissues. Although urea always exists in the blood, its quantity is less than in the lymph.

According to Ludwig and Hammersten, the lymph of the dog contains about forty parts per hundred in volume of carbon dioxide, of which seventeen parts may be extracted by the air-pump and twenty-three parts, by acids. In addition, the lymph contains a trace of oxygen and one or two parts of nitrogen.

FIG. 98.—*Chyle taken from the lacteals and thoracic duct of a criminal executed during digestion* (Funke).
This figure shows the leucocytes and excessively fine granules of fatty emulsion.

*Corpuscular Elements of the Lymph.*—In every part of the lymphatic system, in addition to a few very minute fatty granules, there are found certain corpuscular elements known as lymph-corpuscles. These exist, not only in the clear lymph, but in the opaque fluid contained in the lacteals during absorption. They are now regarded as identical with the white blood-corpuscles, or leucocytes. Eight thousand two hundred leucocytes have been counted in 0·061 cubic inch (1 c. c.) of lymph from a dog (Ritter).

The leucocytes found in the lymph and chyle are rather less uniform in size and general appearance than the white corpuscles of the blood. Their average diameter is about $\frac{1}{2500}$ of an inch (10 $\mu$.); but some are larger, and others are as small as $\frac{1}{5000}$ of an inch (5 $\mu$.). Some of these corpuscles are quite clear and transparent, presenting but few granulations and an indistinct nuclear appearance in their centre; but others are granular and quite opaque. They present the same adhesive character in the lymph as in the blood, and frequently they are found collected in masses in different parts of the lymphatic system. In all other regards, these bodies present the same characters as the leucocytes of the blood, and they need not, therefore, be farther described.

In addition to the ordinary leucocytes and a certain number of fatty granules, a few small, clear globules or granules, about $\frac{1}{7500}$ of an inch (3·3 $\mu$.)

in diameter, called sometimes globulins, are almost constantly present in the lymph. These are insoluble in ether and acetic acid but are dissolved by ammonia. They were regarded by Robin as a variety of leucocytes and described by him as free nuclei.

*Origin and Uses of the Lymph.*—There can hardly be any doubt concerning the source of most of the liquid portions of the lymph, for they can be derived only from the blood. Although the exact relations between the smallest lymphatics and the blood-vessels have not been made out in all parts of the system, there is manifestly no anatomical reason why the water, mixed with albuminoid matters and holding salts in solution, should not pass from the blood into the lymphatics; and this is rendered nearly certain by the fact that the lymphatics surround many of the blood-vessels. In comparing the composition of the lymph with that of the plasma of the blood, it is seen that the constituents of these fluids are nearly if not quite identical; the only variations being in their relative proportions. This is another argument in favor of the passage of most of the constituents of the blood into the lymph.

One of the most important physiological facts in the chemical history of the lymph is the constant existence of a considerable proportion of urea. This can not be derived from the blood, for its proportion is greater in the lymph, notwithstanding the fact that this fluid is being constantly discharged into the blood-vessels. The urea which exists in the lymph is derived from the tissues; it is discharged then into the blood, and is constantly being removed from this fluid by the kidneys.

The positive facts upon which to base any precise ideas with regard to the general office of the lymph are not very many. From the composition of this fluid, its mode of circulation, and the fact that it is being constantly discharged into the blood, it would not seem to have an important use in the active processes of nutrition. The experiments of Collard de Martigny sustain this view, inasmuch as the quantity and the proportion of solid constituents of the lymph were rather increased than diminished in animals that had been deprived of food and drink for several days; while it is well known that starvation always impoverishes the blood from the first. On the other hand, urea, one of the most important of the products of disassimilation, is undoubtedly taken up by the lymph and conveyed in this fluid to the blood. It remains for future investigations to determine whether other excrementitious matters may not be taken up from the tissues in the same way—a question of importance in its relations to the mechanism of excretion.

What is positively known with regard to the uses of the lymph may be summed up in a very few words: A great part of its constituents is evidently derived from the blood, and the relations of these to nutrition are not understood. The same may be said of sugar, which is a constant constituent of the lymph. Urea and perhaps other excrementitious matters are taken up from the tissues by the lymph, and are discharged into the blood, to be removed from the system by the appropriate organs.

*Properties and Composition of Chyle.*—During the intervals of digestion, the intestinal lymphatics and the thoracic duct carry ordinary lymph; but as soon as absorption of alimentary matters begins, certain nutritive matters are taken up in quantity by these vessels, and their contents are known under the name of chyle.

In the human subject and in carnivorous animals, the chyle, taken from the lacteals near the intestine, where it is nearly pure, or from the thoracic duct, when it is mixed with lymph, is a white, opaque, milky fluid, of a slightly saline taste and an odor which is said to resemble that of the semen. The odor is also said to be characteristic of the animal from which the fluid is taken; although this is not very marked, except on the addition of a concentrated acid, the process employed by Barreul to develop the characteristic odor in the fluids from different animals. Bouisson has found that the peculiar odor of the dog was thus developed in fresh chyle taken from the thoracic duct.

The reaction of the chyle is either alkaline or neutral. Dalton noted an alkaline reaction in the chyle of the goat and of the dog; and a specimen of chyle taken from a criminal immediately after execution, examined by Rees, was neutral. Leuret and Lassaigne obtained the fluid from the receptaculum chyli in a man that had died of cerebral inflammation, and found its reaction to be alkaline.

The specific gravity of the chyle is always less than that of the blood; but it is very variable and depends upon the quality of the food and particularly upon the quantity of liquids ingested. Lassaigne found the specific gravity of a specimen of pure chyle taken from the mesenteric lacteals of a bull to be 1013, and the specific gravity of the specimen of human chyle examined by Rees was 1024.

The differences in the appearance of the chyle in different animals depend chiefly upon the food. Colin found the chyle milky in the carnivora, especially after fats had been taken in quantity; while in dogs that were nourished with articles containing but little fat, its appearance was hardly lactescent. Tiedemann and Gmelin found the chyle almost transparent in herbivora fed with hay or straw. They also observed that the chyle was nearly transparent in dogs fed with liquid albumen, fibrin, gelatine, starch and gluten; while it was white in the same animals fed with milk, meat, bones etc.

It is impossible to give an accurate estimate of the entire quantity of pure chyle taken up by the lacteal vessels. When it finds its way into the thoracic duct, it is mingled immediately with all the lymph from the lower extremities; and the large quantities of fluid which have been collected from this vessel by Colin and others give no idea of the quantity of chyle absorbed from the intestinal canal. No attempt will be made, therefore, to give even an approximate estimate of the absolute quantity of chyle; but it is evident that this is variable, depending upon the nature of the food and the quantity of liquids ingested.

Like the lymph, the chyle, when removed from the vessels, undergoes coagulation. Different specimens of the fluid vary very much as regards the rapidity with which coagulation takes place. The chyle from the thoracic duct generally coagulates in a few minutes. The first portion of the fluid collected from the human subject by Rees—the chyle was collected in this case in two portions—coagulated in an hour. Received into an ordinary glass vessel, the chyle generally separates more or less completely after coagulation, into clot and serum. The serum is quite variable in quantity and is never clear. Its milkiness does not depend entirely upon the presence of particles of emulsified fat, and it is not rendered transparent by ether. It contains, also, a number of leucocytes and organic granules.

Observations have been made with reference to the influence of different kinds of food upon the chyle; but these have not been followed by any definite results that can be applied to the human subject. It is usual to find the chyle fluid in the lacteals and in the thoracic duct for many hours after death; but it soon coagulates after exposure to the air. Although the entire lacteal system is sometimes found, in the human subject and in the inferior animals, filled with perfectly opaque, coagulated chyle, the fluid does not often coagulate in the vessels.

*Composition of the Chyle.*—Analyses of the milky fluid taken from the thoracic duct during full digestion by no means represent the composition of pure chyle; and it is only by collecting the fluid from the mesenteric lacteals, that it can be obtained without a very large admixture of lymph. In the human subject, it is rare even to have an opportunity of taking the fluid from the thoracic duct in cases of sudden death during digestion; and in most of the inferior animals which have been operated upon, it is difficult to obtain fluid from the small lacteals in quantity sufficient for accurate analysis. In operating upon the ox, however, Colin has succeeded in collecting pure chyle in considerable quantity.

In the analysis by Rees, the fluid was taken from the thoracic duct of a vigorous man, a little more than an hour after his execution by hanging. The subject was apparently in perfect health to the moment of his death. The evening before, he ate two ounces (56·7 grammes) of bread and four ounces (113·4 grammes) of meat. At seven A. M., precisely one hour before death, he took two cups of tea and a piece of toast; and he drank a glass of wine just before mounting the scaffold. When the dissection was made, the body was yet warm, although the weather was quite cold. The thoracic duct was rapidly exposed and divided, and about six fluidrachms (22·2 c. c.) of milky chyle were collected. The fluid was neutral and had a specific gravity of 1024. The following was its approximate composition:

COMPOSITION OF HUMAN CHYLE FROM THE THORACIC DUCT.

| | |
|---|---|
| Water | 904·8 |
| Albumen, with traces of fibrinous matter | 70·8 |
| Aqueous extractive | 5·6 |
| Alcoholic extractive, or osmazome | 5·2 |
| Alkaline chlorides, carbonates and sulphates, with traces of alkaline phosphates and oxides of iron | 4·4 |
| Fatty matters | 9·2 |
| | 1,000·0 |

Of the constituents of the chyle not given in the ordinary analyses, the most important are the urea, which in all probability is derived exclusively from the lymph, and sugar, coming from the saccharine and amylaceous articles of food during digestion.

The difference in chemical composition between the unmixed lymph and the chyle is illustrated in a comparative examination of these two fluids taken from a donkey. The fluids were collected by Lane, the chyle being taken from the lacteals before reaching the thoracic duct. The animal was killed seven hours after a full meal of oats and beans. The following analyses of the fluids were made by Rees:

COMPOSITION OF CHYLE AND LYMPH BEFORE REACHING THE THORACIC DUCT.

| | Chyle. | Lymph. |
|---|---|---|
| Water | 902·37 | 965·36 |
| Albuminous matter | 35·16 | 12·00 |
| Fibrinous matter | 3·70 | 1·20 |
| Animal extractive matter soluble in water and alcohol | 3·32 | 2·40 |
| Animal extractive matter soluble in water only | 12·33 | 13·19 |
| Fatty matter | 36·01 | a trace |
| Salts, { Alkaline chlorides, sulphates and carbonates, with traces of alkaline phosphates and oxide of iron. } | 7·11 | 5·85 |
| | 1,000·00 | 1,000·00 |

The above analyses show a very marked difference in the proportion of solid constituents in the two fluids. The chyle contains about three times as much albumen and fibrin as the lymph, with a larger proportion of salts. The proportion of fatty matters in the chyle is very great, while in the lymph there exists only a trace. The individual constituents of the chyle given in the above tables do not demand any farther consideration than they have already received under the head of lymph. The albuminoid matters are in part derived from the food, and in part from the blood, through the admixture of the chyle with lymph. The fatty matters are derived in greatest part from the food. As far as has been ascertained by analyses of the chyle for salts, this fluid has been found to contain essentially the same inorganic constituents as the plasma of the blood.

The presence of sugar in the chyle was first mentioned by Brande, who described it, however, rather indefinitely. Glucose was first distinctly recognized in the chyle by Trommer, and its existence in many of the higher orders of animals has since been fully established by Colin.

*Microscopical Characters of the Chyle.*—The milky appearance of the chyle as contrasted with the lymph is due to the presence of a large number of very minute fatty granules. The liquid becomes much less opaque when treated with ether, which dissolves many of the fatty particles. In fact, the chyle of the thoracic duct is nothing more than lymph to which an emulsion of fat in a liquid containing albuminoid matters and salts is temporarily added during the process of intestinal absorption. The quantity of fatty granules in the chyle varies considerably with the diet, and it generally diminishes progressively from the smaller to the larger vessels, on account of the constant admixture of lymph. The size of the granules is pretty uniformly $\frac{1}{25000}$ to $\frac{1}{12500}$ of an inch (1 to 2 $\mu$). They are much smaller and more uniform in size in the lacteals than in the cavity of the intestine. Their constitution is not constant; and they are composed of the different varieties of fat which are taken as food, mixed with each other in various proportions. The ordinary corpuscular elements of the lymph, leucocytes and globulins, are also found in variable quantity in the chyle.

### Movements of the Lymph and the Chyle.

Compared with the current of blood, the movements of the lymph and chyle are feeble and irregular; and the character of these movements is such that they are evidently due to a variety of causes. As regards those constituents which are derived directly from the blood, the lymph may be said to undergo a true circulation; inasmuch as there is a constant transudation at the peripheral portion of the vascular system, of fluids which are returned to the circulating blood by the communications of the lymphatic system with the great veins. The constituents of the lymph, however, are not derived entirely from the blood, a considerable portion resulting from interstitial absorption in the general lymphatic system; and the chyle contains certain nutritive matters absorbed by the lacteal vessels. These are, physiologically, the most important constituents of the lymph and chyle; and they are taken up simply to be carried to the blood and do not pass again from the general vascular system into the lymphatics.

As far as the mode of origin of the lymph and chyle has any bearing upon the movements of these fluids in the lymphatic vessels, there is no difference between the imbibition of new matters from the tissues or from the intestinal canal and the transudation of the liquid portions of the blood; for the mechanism of the passage of liquids from the blood-vessels is such that the motive power of the blood can not be felt. An illustration of this is in the mechanism of the transudation of the liquid portions of the secretions. The force with which fluids are discharged into the ducts of the glands is very great and is independent of the action of the heart, being due entirely to the processes of transudation and secretion. This is combined with the force of imbibition, and with it forms one of the important agents in the movements of the lymph and chyle. These movements are studied with great difficulty. One of the first peculiarities to be observed is that under normal conditions, the vessels are seldom distended, and the quantity of fluid which they contain is subject to considerable variation. As far as the flow in the vessels of medium size is concerned, the movement is probably continuous, subject only to certain momentary obstructions or accelerations from various causes; but in the large vessels situated near the thorax and in those within the chest, the movements are in a marked degree remittent, or they may even be intermittent. All experimenters who have observed the flow of lymph or chyle from a fistula into the thoracic duct have noted a constant acceleration with each act of expiration; and an impulse synchronous with the pulsations of the heart has frequently been observed.

The fact that the lymphatic system is never distended, and the existence of the valves, by which different portions may become isolated, render it impossible to estimate the general pressure of fluid in these vessels. This is undoubtedly subject to great variations in the same vessels at different times, as well as in different parts of the lymphatic system. It is well known, for example, that the degree of distention of the thoracic duct is very variable, its capacity not infrequently being many times increased during active absorption. At the same time it is difficult to attach a manometer to any part of the lymphatic system without seriously obstructing the circulation and consequently exaggerating the normal pressure; but the force with which liquids penetrate these vessels is very great. This is illustrated by the experiment of tying the thoracic duct; for after this operation, unless communicating vessels exist by which the fluids can be discharged into the venous system, their accumulation is frequently sufficient to rupture the vessel.

The general rapidity of the current in the lymphatic vessels has never been accurately estimated. As a natural consequence of the variations in the distention of these vessels, the rapidity of the circulation must be subject to constant modifications. Béclard, making his calculation from the experiments of Colin, who noted the quantity of fluid discharged in a given time from fistulous openings into the thoracic duct, estimated that the rapidity of the flow in this vessel was about one inch (25·4 mm.) per second. This estimate, however, can be only approximate; and it is evident that the flow must be much less rapid in the vessels near the periphery than in the large trunks, as the liquid moves in a space which becomes rapidly contracted as it approaches the openings into the venous system.

Various influences combine to produce the movements of fluids in the lymphatic system, some being constant in their operation, and others, intermittent or occasional. These will be considered, as nearly as possible, in the order of their relative importance.

The forces of endosmosis and transudation are undoubtedly the main causes of the lymphatic circulation, more or less modified, however, by influences which may accelerate or retard the current; but this action is capable in itself of producing the regular movement of the lymph and chyle. It is a force which is in constant operation, as is seen in cases of ligation of the thoracic duct, a procedure which must finally abolish all other forces which aid in producing the lymphatic circulation. When the receptaculum chyli is ruptured as a consequence of obstruction of the thoracic duct, the vessel gives way as the result of the constant endosmotic action, in the same way that the exposed membranes of an egg may be ruptured by endosmosis, when immersed in water.

The situations in which the endosmotic force originates are at the periphery, where the single wall of the vessels is very thin, and where the extent of absorbing surface is large. If liquids can penetrate with such rapidity and force through the walls of the blood-vessels, where their entrance is opposed by the pressure of the fluids already in their interior, they certainly must pass without difficulty through the walls of the lymphatics, where there is no lateral pressure to oppose their entrance, except that produced by the weight of the column of liquid. This pressure is readily overcome; and the valves in the lymphatic system effectually prevent any backward current.

In describing the anatomy of the lymphatic system, it has already been stated that the large vessels and those of medium size are provided with non-striated muscular fibres and are endowed with contractility. This fact has been demonstrated by physiological as well as anatomical investigations. Béclard stated that he often produced contractions of the thoracic duct by the application of the two poles of an inductive apparatus. It is not uncommon to see the lacteals become reduced in size to a mere thread, even while under observation. Although experiments have generally failed to demonstrate any regular, rhythmical contractions in the lymphatic system, it is probable that the vessels contract upon their contents, when they are unusually distended, and thus assist the circulation, the action of the valves opposing a regurgitating current. This action, however, can not have any considerable and regular influence upon the general current.

Contractions of the ordinary voluntary muscles, compression of the abdominal organs by contraction of the abdominal muscles, peristaltic movements of the intestines and pulsations of large arteries situated against the lymphatic trunks, particularly the thoracic aorta, are all capable of increasing the rapidity of the circulation of the lymph and chyle.

The contractions of voluntary muscles assist the lymphatic circulation in precisely the way in which they influence the flow of blood in the venous system; and there is nothing to be added regarding this action to what has already been said on this subject in connection with the description of the venous circulation.

Increase in the flow of chyle in the thoracic duct, as the result of compression of the abdominal organs or of kneading the abdomen with the hands, was observed by Magendie, and the fact has been confirmed in all recent experiments on this subject. The same effect, though probably less in degree, is produced by the peristaltic contractions of the intestines.

When a tube is introduced into the upper part of the thoracic duct, it is frequently the case that the fluid is discharged with increased force at each pulsation of the heart. This was frequently observed by Dalton in his experiments on the thoracic duct, and he described the jets as being "like blood coming from a small artery when the circulation is somewhat impeded." This impulse is due to compression of the thoracic duct as it passes under the arch of the aorta. Its influence upon the general current of the lymph and chyle is probably insignificant.

While the *vis a tergo* must be regarded as by far the most important agent in the production of the lymphatic circulation, the movements of fluids in the thoracic duct receive constant and important aid from the respiratory acts. This fact has long been recognized; and in the works of

Haller there is a full discussion of the influence of the diaphragm and of the movements of the thorax upon the circulation of chyle. Colin always found marked impulses in the flow of chyle from a fistula into the thoracic duct, which were synchronous with the movements of respiration. With each act of expiration the fluid was forcibly ejected, and with inspiration the flow was very much diminished or even arrested. These impulses became much more marked when respiration was interfered with and the efforts became violent. The impulses were sometimes so decided, that the pulsations were repeated in a long elastic tube attached to the canula for the purpose of collecting the fluid.

From all these considerations, it is evident that although there are many conditions capable of modifying the currents in the lymphatic system, the regular flow of the lymph and chyle depends chiefly upon the *vis a tergo*; but the vessels themselves sometimes undergo contraction, and they are subject to occasional compression from surrounding parts, which, from the existence of valves in the vessels, must favor the current toward the venous system. The alternate dilatation and compression of the thoracic duct with the acts of respiration likewise aid the circulation, and they are more efficient than any other force, except the *vis a tergo*. The action of the valves is precisely the same in the lymphatic as in the venous system.

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## CHAPTER XI.

### *SECRETION.*

Classification of the secretions—Mechanism of the production of the true secretions—Mechanism of the production of the excretions—Influence of the composition and pressure of the blood on secretion—Influence of the nervous system on secretion—Anatomical classification of glandular organs—Classification of the secreted fluids—Synovial membranes and synovia—Mucous membranes and mucus—Physiological anatomy of the sebaceous, ceruminous and Meibomian glands—Ordinary sebaceous matter—Smegma of the prepuce and of the labia minora—Vernix caseosa—Cerumen—Meibomian secretion—Mammary secretion—Physiological anatomy of the mammary glands—Mechanism of the secretion of milk—Conditions which modify the lacteal secretion—Quantity of milk—Properties and composition of milk—Microscopical characters of milk—Composition of milk—Variations in the composition of milk—Colostrum—Lacteal secretion in the newly-born—Secretory nerve-centres.

THE processes of secretion are intimately connected with general nutrition. In the sense in which the term secretion is usually received, it embraces most of the processes in which there is a separation of matters from the blood by glandular organs or a formation of a new fluid out of materials furnished by the blood. The blood itself, the lymph and the chyle, are in no sense to be regarded as secretions. These fluids, like the tissues, are permanent parts of the organism, undergoing those changes only that are necessary to their proper regeneration. They are likewise characterized by the presence of certain formed anatomical elements, which themselves undergo processes of molecular destruction and regeneration. These characters are not possessed by the secretions. As a rule, the latter are homogeneous fluids, without formed anatomical elements, except as accidental constituents, such as the desquamated epithelium in mucus or in sebaceous matter. The secretions are either discharged from the body, when they are called excretions, or after having performed their proper office as secretions, are absorbed in a more or less modified form by the blood.

Physiologists now regard secretion as the act by which fluids, holding certain substances in solution, and sometimes containing peculiar ferments but not necessarily possessing formed anatomical elements, are separated from the blood or are formed by special organs out of materials furnished by the blood. These organs may be membranes, follicles or collections of follicles, or tubes. In the latter instances they are called glands. The liquids thus formed are called secretions; and they may be destined to perform some office connected with nutrition or may be simply discharged from the organism.

It is not strictly correct to speak of formed anatomical elements as products of secretion, except in the instance of the fatty particles in the milk. The leucocytes found in pus, the spermatozoids of the seminal fluid, and the ovum, which are sometimes spoken of as products of secretion, are anatomical elements developed in the way in which such structures are ordinarily formed. For example, leucocytes, or pus-corpuscles, may be developed without the intervention of any special secreting organ; and spermatozoids and ova are generated in the testicles and the ovaries, by a process entirely different from ordinary secretion. It is important to recognize these facts in studying the mechanism by which the secretions are produced.

*Classification of the Secretions.*—Certain secretions are formed by special organs and have important uses which do not involve their discharge from the body. These may be classed as the true secretions; and the most striking examples of such are the digestive fluids. Each one of these fluids is formed by a special gland or set of glands, which generally has no other office; and they are never produced by any other part. It is the gland which produces the characteristic constituent or constituents of the true secretions, out of materials furnished by the blood; and the matters thus formed never pre-exist in the circulating fluid. The office which these fluids have to perform is generally not continuous; and when this is the case, the flow of the secretion is intermittent, taking place only when its action is required. When the parts which produce one of the true secretions are destroyed, as is sometimes done in experiments upon living animals, the characteristic constituents of this particular secretion never accumulate in the blood nor are they formed vicariously by other organs. The simple effect of such an experiment is absence of the secretion, with the disturbances consequent upon the loss of its physiological action.

Certain other of the fluids are composed of water, holding one or more characteristic constituents in solution, which result from the physiological wear of the tissues. These matters have no office to perform in the animal economy and are simply separated from the blood to be discharged from the body. These may be classed as excretions, the urine being the type of fluids of this kind. The characteristic constituents of the excrementitious fluids are formed in the tissues, as one of the results of the constant changes going on in all organized, living structures. They always pre-exist in the circulating fluid and may be eliminated, either constantly or occasionally, by a number of organs. As they are produced continually in the substance of the tissues and are taken up by the blood, they are constantly separated from the blood by the proper eliminating organs. When the glands which thus eliminate these substances are destroyed or when their action is seriously impaired, the excrementitious matters may accumulate in the blood and give rise to certain toxic phenomena. These effects, however, are often retarded by the vicarious action of other organs.

There are some fluids, as the bile, which have important uses as secretions, and which nevertheless contain certain excrementitious matters. In these instances, it is only the excrementitious matters that are discharged from the organism.

In the sheaths of some tendons and of muscles, in the substance of muscles and in some other situations, fluids are found which simply moisten the parts and which contain very little organic matter, with but a small proportion of inorganic salts. Although these are frequently spoken of as secretions, they are produced generally by a simple, mechanical transudation of certain of the constituents of the blood through the walls of the vessels. Still, it is difficult to draw a line rigorously between transudation and some of the phenomena of secretion; particularly as experiments upon dialysis have shown that simple, osmotic membranes are capable of separating complex solutions, allowing certain constituents to pass much more freely than others. This fact explains why the transuded fluids do not contain all the soluble constituents of the blood in the proportions in which they exist in the plasma. All the secreted fluids, both the true secretions and the excretions, contain many of the inorganic salts of the blood-plasma.

*Mechanism of the Production of the True Secretions.*—Although the characteristic constituents of the true secretions are not to be found in the blood or in any other of the animal fluids, they can generally be extracted from the glands, particularly during their intervals of so-called repose. This fact has been repeatedly demonstrated with regard to many of the digestive fluids, as the saliva, the gastric juice and the pancreatic juice; and artificial fluids, possessing certain of the physiological properties of the natural secretions, have been prepared by simply extracting the glandular tissue with water. There can be no doubt, therefore, that during the periods when the secretions are not discharged, the glands are taking from the blood matters which are to be transformed into the characteristic constituents of the individual secretions, and that this process is constant, bearing a close resemblance to the general act of nutrition. There are certain anatomical elements in the glands, which have the power of selecting the proper materials from the blood and causing them to undergo peculiar transformations; in the same way that the muscular tissue takes from the nutritive fluid albuminoid matters and transforms them into its own substance. The exact nature of this property is unexplained.

In all of the secreting organs, epithelium is found which seems to possess the power of forming the peculiar constituents of the different secretions. The epithelial cells lining the tubes or follicles of the glands constitute the only peculiar structures of these parts, the rest being made up of basement-membrane, connective tissue, blood-vessels, nerves, and other structures which are distributed generally in the economy; and these cells alone contain the constituents of the secretions. It has been found, for example, that the liver-cells contain the glycogen formed by the liver; and it has been farther shown that when the cellular structures of the pancreas have been destroyed, the secretion is no longer produced. There can be hardly any doubt with regard to the application of this principle to the glands generally, both secretory and excretory. Indeed, it is well known to pathologists, that when the tubes of the kidney have become denuded of their epithelium, they are no longer capable of separating from the blood the peculiar constituents of the urine.

With regard to the origin of the characteristic constituents to the true secretions, it is impossible to entertain any other view than that they are produced in the epithelial structures of the glands. While the secretions contain inorganic salts in solution transuded from the blood, the organic constituents, such as ptyaline, pepsine, trypsine etc., are readily distinguished from all other albuminoid substances, by their peculiar physiological properties.

It may be stated, then, as a general proposition, that the characteristic constituents of the true secretions, as contradistinguished from the excretions, are formed by the epithelial structures of the glands, out of materials furnished mainly by the blood. Their formation is by no means confined to what is usually termed the period of activity of the glands, or the time when the secretions are poured out, but it takes place more or less constantly when no fluid is discharged. It is more than probable, indeed, that the formation of the peculiar and characteristic constituents of the secretions takes place with as much activity in the intervals of secretion as during the discharge of fluid; and most of the glands connected with the digestive system seem to require certain intervals of repose and are capable of discharging their secretions for a limited time only.

When a secreting organ is called into activity—like the gastric mucous membrane or the pancreas, upon the introduction of food into the alimentary canal—a marked change in its condition takes place. The circulation in the part is then very much increased in activity, thus furnishing water and the inorganic constituents of the secretion. This difference in the quantity of blood in the glands during their activity is very marked when the organs are exposed in a living animal, and is one of the important facts bearing upon the mechanism of secretion.

In all the secretions proper, there are intervals, either of complete repose, as is the case with the gastric juice or the pancreatic juice, or periods when the activity of the secretion is very greatly diminished, as in the saliva. These periods of repose seem to be necessary to the proper action of the secreting glands; forming a marked contrast with the constant action of organs of excretion. It is well known, for example, that digestion is seriously disturbed when the act is too prolonged on account of the habitual ingestion of an excessive quantity of food.

From the considerations already mentioned, it is evident that the characteristic constituents of the true secretions are formed by the epithelial structures of the glands. While the mechanism of this process is not understood in all its details as regards all of the secretions, in some of the glands the processes have been studied with tolerably definite results. In some of the salivary glands, in the peptic cells and in the cells of the pancreas, it has been shown that the so-called ferments are not formed directly. The secreting cells are apparently divided into two portions, or zones; an outer zone, which is next the tubular membrane, and an inner zone, next the lumen of the tube or follicle. In the inner zone, during the intervals of actual secretion, there appears a substance, which at the time when the secretion is formed and is poured out, is changed into the true ferment, or active principle of the secretion; so that there is probably a zymogenic, or ferment-forming substance, first produced by the cells. The substance, if such a substance exists, out of which ptyaline is formed, has not been described; but in the viscid forms of saliva, there appears to be first formed a substance called mucinogen, afterward changed into mucine, upon which the viscidity of the fluid depends.

In the salivary glands which produce viscid secretions, the submaxillary and sublingual, the parenchyma presents two kinds of acini, serous and mucous. The so-called serous acini are the more abundant and are thought to produce the true saliva, while the mucous acini secrete the viscid constituents of the saliva.

In the production of pepsine, the inner zone of the peptic cells first forms pepsinogen, which is changed into pepsine as it is discharged from the glands. In the pancreas, trypsinogen is formed in the inner zone of the cells, and this is changed into trypsine. The general name zymogen has been given to the substances which are changed into the digestive ferments; although, as is evident, this substance is not identical in the different glands. The formation of the ferments of the true secretions is analogous in its nature to certain of the nutritive processes.

The theory that the discharge of the secretions is due simply to mechanical causes and is attributable solely to the increase in the pressure of blood can not be sustained. Pressure undoubtedly has considerable influence upon the activity of secretion; but the flow will not always take place in obedience to simple pressure, and secretion may be excited for a limited time without any increase in the quantity of blood circulating in the gland.

The glands possess a peculiar excitability, which is manifested by their action in response to proper stimulation. During secretion, they generally receive an increased quantity of blood; but this is not indispensable, and secretion may be excited without any modification of the circulation. This excitability will disappear when the artery supplying the part with blood is tied for a number of hours; and secretion can not then be excited even when the blood is again allowed to circulate. If the gland be not deprived of blood for too long a period, the excitability is soon restored; but it may be permanently destroyed by depriving the part of blood for a long time. These facts show a certain similarity between glandular and muscular excitability, although these properties are manifested in very different ways.

*Mechanism of the Production of the Excretions.*—Certain of the glands separate from the blood excrementitious matters which are of no use in the economy and are simply discharged from the body. These matters, which will be fully considered, both in connection with the fluids of which they form a part and under the head of nutrition, are entirely different in their mode of production from the characteristic constituents of the secretions. The formation of excrementitious matters takes place in the tissues and is connected with the general process of nutrition; and in the excreting glands there is simply a separation of products already formed. The action of the excreting organs is constant, and there is not that regular, periodic increase in the activity of the circulation which is observed in secreting organs; but it has been observed that the blood which comes from the kidneys is nearly as red as arterial blood, showing that the quantity of blood which these organs receive is greater than is required for mere nutrition, the excess, as in the secreting organs, furnishing the water and inorganic salts that are found in the urine. It has also been shown that when the secretion of urine is interrupted, the blood of the renal veins becomes dark like the blood in the general venous system.

Excretion is not, under all conditions, confined to the ordinary excretory organs. When their action is disturbed, certain of the secreting glands, as the follicles of the stomach and intestine, may for a time eliminate excrementitious matters; but this is abnormal and is analogous to the elimination of foreign matters from the blood by the glands.

*Influence of the Composition and Pressure of the Blood upon Secretion.*—Under normal conditions, the composition of the blood has little to do with the action of the secreting organs, as it simply furnishes the materials out of which the characteristic constituents of the secretions are formed; but when certain foreign matters are taken into the system or are injected into the blood-vessels, they are eliminated by the different glandular organs, both secretory and excretory. These organs seem to possess a power of selection in the elimination of different substances. Thus, sugar and potassium ferrocyanide are eliminated in greatest quantity by the kidneys; the salts of iron, by the kidneys and the gastric tubules; and iodine, by the salivary glands.

The discharge of secretions is almost always accompanied with an increase in the pressure of blood in the vessels supplying the glands; and it has been shown, on the other hand, that an exaggeration in the pressure, if the nerves of the glands do not exert an opposing influence, increases the activity of secretion. The experiments of Bernard on this point show the influence of pressure upon the salivary and renal secretions, particularly the latter. After inserting a tube into one of the ureters of a living animal, so that the activity of the renal secretion could be accurately observed, the pressure in the renal artery was increased by tying the crural and the brachial. It was then found that the flow of urine was markedly increased. The pressure was afterward diminished by the abstraction of blood, which was followed by a corresponding diminution in the quantity of urine. The same phenomena were observed in analogous experiments upon the submaxillary secretion. These facts, however, do not demonstrate that secretion is due simply to an increase in the pressure of blood in the glands, although this undoubtedly exerts an important influence. It is necessary that every condition should be favorable to the act of secretion for this influence to be effective. Experiments have shown that pain may completely arrest the secretion of urine, operating undoubtedly through the nervous system. If the flow of urine be arrested by pain, an increase in the pressure of blood in the part fails to excite the secretion.

*Influence of the Nervous System on Secretion.*—The fact that the secretions are generally intermittent in their flow, being discharged in obedience to impressions which are made only when there is a demand for their physiological action, would naturally lead to the supposition that they are regulated, to a great extent, through the nervous system; particularly as it is now well established that the nerves are capable of modifying and regulating local circulations. The same facts apply, to a certain extent, to the excretions, which are also subject to considerable modifications.

It is evident that the nervous system has an important influence in the production of the secretions; and this is exerted largely through modifications in the activity of the circulation in the glands. This takes place in greatest part through vaso-motor nerves distributed to the muscular coats of the arteries of supply. When these nerves are divided, the circulation is increased here, as in other situations, and secretion is the result; and if the extremity of the nerve connected with the gland be stimulated, contraction of the vessels follows, and the secretion is arrested.

With regard to many of the glands, it has been shown that the influence of the vaso-motor nerves is antagonized by certain other nerves, which latter are called the motor nerves of the glands. The motor nerve of the submaxillary is the chorda tympani; and as both this nerve and the sympathetic, which latter contains the vaso-motor filaments, together with the excretory duct of the gland, can be easily exposed and operated upon in a living animal, many experiments have been performed upon this gland. When all these parts are exposed and a tube is introduced into the salivary duct, division of the sympathetic induces secretion, with an increase in the circulation in the gland, the blood in the vein becoming red. On the other hand, division of the chorda tympani, the sympathetic being intact, arrests secretion, and the venous blood coming from the gland becomes dark. If the nerves be now stimulated alternately, it will be found that stimulation of the sympathetic produces contraction of the vessels of the gland and arrests secretion, while a stimulus applied to the chorda tympani increases the circulation and excites secretion (Bernard). Enough is known of the nervous influences which modify secretion, to admit of the inference that all the glands are supplied with nerves through which certain reflex phenomena, affecting their secretions, take place.

As reflex phenomena involve the action of nerve-centres, it becomes a question to determine whether any particular parts of the central nervous system preside over the various secretions. Experiments showing the existence of such centres are not wanting, but it will be more convenient to treat of these in connection with the physiology of the individual secretions.

Mental emotions, pain, and various conditions, the influence of which upon secretion has long been observed, operate through the nervous system. Many familiar instances of this kind are mentioned in works on physiology: such as the secretion of tears; arrest or production of the salivary secretions; sudden arrest of the secretion of the mammary glands, from violent emotion; increase in the secretion of the kidneys or of the intestinal tract, from fear or anxiety; with other examples which it is unnecessary to enumerate.

*Paralytic Secretion by Glands.*—The effects of destruction of the nerves distributed to the parenchyma of some of the glandular organs are very remarkable. Müller and Peipers destroyed the nerves distributed to the kidney and found that not only was the secretion arrested in the great majority of instances, but the renal tissue became softened and broken down. Bernard found that animals operated upon in this way died, and that the tissue of the kidney was broken down into a fetid, semi-fluid mass. After division of the nerves of the salivary glands, the organs became atrophied, but they did not undergo the peculiar putrefactive change which was observed in the kidneys. The same effect was produced when the nerves were paralyzed by introducing a few drops of a solution of curare at the origin of the little artery which is distributed to the submaxillary gland. It is possible that other glands have so-called motor-nerves, stimulation of which excites secretion, but such nerves have been most satisfactorily isolated and studied in connection with the salivary secretions. When the motor-nerves of the salivary glands are divided, in the course of a day or two, the secretion becomes abundant and watery, losing its normal characters. After about eight days, the secretion begins to diminish and the glands undergo atrophy. The increased secretion first observed has been called "paralytic." The watery secretion discharged from a permanent pancreatic fistula is thought to be paralytic; and certainly it does not present the physiological properties of normal pancreatic juice.

*Anatomical Classification of Glandular Organs.*—The organs which produce the different secretions are susceptible of a classification according to their anatomical peculiarities, which greatly facilitates their study. They may be divided as follows:

1. *Secreting membranes.*—Examples of these are the synovial membranes.

2. *Follicular glands.*—Examples of these are the simple mucous follicles, the follicles of Lieberkühn and the uterine follicles.

3. *Tubular glands.*—Examples of these are the ceruminous glands, the sudoriparous glands and the kidneys.

4. *Racemose glands, simple and compound.*—Examples of the simple racemose glands are the sebaceous and Meibomian glands, the tracheal glands and the glands of Brunner. Examples of the compound racemose glands are the salivary glands, the pancreas, the lachrymal glands and the mammary glands.

5. *Ductless, or blood-glands.*—Examples of these are the thymus, the thyroid, the supra-renal capsules and the spleen.

The liver is a glandular organ which can not be placed in any one of the above divisions. The lymphatic glands and other parts connected with the lymphatic and the lacteal system are not true glandular organs; and these are sometimes called conglobate glands.

The general structure of secreting membranes and of the follicular glands is very simple. The secreting parts consist of a membrane, generally homogeneous, covered on the secreting surface with epithelial cells. Beneath this membrane, ramify the blood-vessels which furnish materials for the secretions. The follicular glands are simply digital inversions of this structure, with rounded, blind extremities, the epithelium lining the follicles.

The tubular glands have essentially the same structure as the follicles, except that the tubes are long and are more or less convoluted. The more complex of these organs contain connective tissue, blood-vessels, nerves and lymphatics.

The compound racemose glands are composed of branching ducts, around the extremities of which are arranged collections of rounded follicles, like bunches of grapes. In addition to the epithelium, basement-membrane and blood-vessels, these organs contain connective tissue, lymphatics, non-striated muscular fibres, and nerves. In the simple racemose glands the excretory duct does not branch.

The ductless glands contain blood-vessels, lymphatics, nerves, sometimes non-striated muscular fibres, and a peculiar structure called pulp, which is composed of fluid with cells and occasionally with closed vesicles. These are sometimes called blood-glands, because they are supposed to modify the blood as it passes through their substance.

The testicles and the ovaries are not simply glandular organs; for in addition to the production of mucous or watery secretions, their principal office is to develop certain anatomical elements, the spermatozoids and the ova. The physiology of these organs will be considered in connection with the physiology of generation.

*Classification of the Secreted Fluids.*—The products of the various glands may be divided, according to their uses, into secretions proper and excretions. Some of the true secretions have certain mechanical uses, and some, like mucus, are thrown off in small quantity without being actually excrementitious; while others, like most of the digestive fluids, are produced at certain intervals and are taken up again by the blood.

TABULAR VIEW OF THE SECRETED FLUIDS.

*Secretions Proper.*

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| Synovia. | Saliva. |
| Mucus, in many varieties. | Gastric juice. |
| Sebaceous matter. | Pancreatic juice. |
| Cerumen, the waxy secretion of the external auditory meatus. | Secretion of the glands of Brunner. |
| Meibomian fluid. | Secretion of the follicles of Lieberkühn. |
| Milk and colostrum. | Secretion of the follicles of the large intestine. |
| Tears. | Bile (also an excretion). |

*Excretions.*

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|---|---|
| Perspiration and the secretion of the axillary glands. | Urine. |
| | Bile (also a secretion). |

*Fluids containing Formed Anatomical Elements.*

Seminal fluid, containing, in addition to spermatozoids, the secretions of a number of glandular structures.
Fluid of the Graafian follicles.

The serous cavities are now regarded as sacs connected with the lymphatic system, and the liquids of these cavities are not classed with the secretions.

*Synovial Membranes and Synovia.*—The true synovial membranes are found in the diarthrodial, or movable articulations; but in various parts of the body are found closed sacs, sheaths etc., which resemble synovial membranes both in structure and in their office. Every movable joint is enveloped in a capsule, which is closely adherent to the edges of the articular cartilage and is even reflected upon its surface for a short distance; but it is now the general opinion that the cartilage which incrusts the articulating extremities of the bones, though bathed in synovial fluid, is not itself covered by a distinct membrane.

The fibrous portion of the synovial membranes is dense and resisting. It is composed of ordinary fibrous tissue, with a few elastic fibres, and blood-vessels. The internal surface is lined with small cells of flattened endothelium with rather large, rounded nuclei. These cells exist in one, two, three or sometimes four layers.

In most of the joints, especially those of large size, as the knee and the hip, the synovial membrane is thrown into folds which contain adipose tissue. In nearly all the joints, the membrane presents fringed, vascular processes, called synovial fringes. These are composed of looped vessels of considerable size; and when injected they bear a certain resemblance to the choroid plexus. The edges of these fringes present a number of leaf-like, membranous appendages, of a great variety of curious forms. They are generally situated near the attachment of the membrane to the cartilage.

The arrangement of the synovial bursæ is very simple. Wherever a tendon plays over a bony surface, there is a delicate membrane in the form of an irregularly shaped, closed sac, one layer of which is attached to the tendon, and the other, to the bone. These sacs are lined with an endothelium like that found in the synovial cavities, and they secrete a true synovial fluid. Bursæ are also found beneath the skin, especially in parts where the integument moves over bony prominences, as the olecranon, the patella and the tuberosities of the ischium. These sacs, sometimes called bursæ mucosæ, are much more common in man than in the inferior animals, and they have essentially the same uses as the deep-seated bursæ. The form of both the superficial and deep-seated bursæ is very irregular, and their interior is frequently traversed by small bands of fibrous tissue. The synovial sheaths, or vaginal processes, line the canals in which the long tendons play, particularly the tendons of the flexors and extensors of the fingers and toes. They have essentially the same structure as the bursæ, and present two layers, one of which lines the canal, while the other is reflected over the tendon. The vascular folds, described in connection with the articular synovial membranes, are found in many of the bursæ and the synovial sheaths.

The quantity of synovia in the joints is sufficient to lubricate freely the articulating surfaces. In a horse of medium size and in good condition, examined immediately after death, Colin found 1·6 fluidrachm (6 c. c.) in the shoulder-joint; 1·9 drachm (7 c. c.) in the elbow-joint; 1·6 drachm (6 c. c.) in the coxo-femoral articulation; 2·2 drachms (8 c. c.) in the femoro-tibial articulation; and 1·9 drachm (7 c. c.) in the tibio-tarsal articulation.

When perfectly normal, the synovial fluid is either colorless or of a pale, yellowish tinge. It is so viscid that it is with difficulty poured from one vessel into another. This peculiar character is due to the presence of an organic substance called synovine. When this organic matter has been extracted and mixed with water, it gives to the fluid the peculiar viscidity of the synovial secretion. The reaction of the fluid is faintly alkaline, on account of the presence of a small proportion of sodium carbonate. The fluid, especially when the joints have been much used, usually contains in suspension pale endothelial cells and a few leucocytes. According to Robin, the synovia of the human subject contains about sixty-four parts per thousand of organic matter, with sodium chloride, sodium carbonate, calcium phosphate and ammonio-magnesian phosphate.

The synovial secretion is produced by the general surface of the membrane and not by any special organs. The folds and fringes which have been described were at one time supposed to be most active in secreting the organic matter, but there is no evidence that they have any such special office.

*Mucous Membranes and Mucus.*—A distinct anatomical division of the mucous membranes may be made into two classes; first, those provided with squamous epithelium, and second, those provided with columnar or conoidal epithelium. All of the mucous membranes line cavities or tubes communicating with the exterior by the different openings in the body.

The following are the principal situations in which the first variety of mucous membranes, covered with squamous epithelium, is found: the mouth, the lower part of the pharynx, the œsophagus, the conjunctiva, the female urethra and the vagina. In these situations the membrane is composed of a chorion made up of inelastic and elastic fibrous tissue, with capillaries, lymphatics and nerves. The elastic fibres are small and quite abundant. The membrane itself is loosely united to the subjacent parts. The chorion is provided with vascular papillæ, more or less marked; but in all situations, except in the pharynx, the epithelial covering fills up the spaces between these papillæ, so that the membrane presents a smooth surface. Between the chorion and the epithelium, is an amorphous basement-membrane. The mucous glands open upon the surface of the membrane by their ducts, but the glandular structure is situated in the submucous tissue. Certain of these glands have been described in connection with the anatomy of the mucous membrane of the mouth, pharynx and œsophagus. They generally are simple racemose glands, presenting a collection of follicles arranged around the extremity of a single excretory duct, and lined or filled with rounded, nucleated epithelium. The squamous epithelium covering these membranes exists generally in several layers and presents great variety, both in form and size. The most superficial layers are of large size, flattened and irregularly polygonal. The deeper layers are smaller and more rounded. The size of these cells is $\frac{1}{2500}$ to $\frac{1}{300}$ of an inch (10 to 83 $\mu$). The cells are pale and slightly granular, each with a small, ovoid nucleus and one or two nucleoli.

The second variety of mucous membranes, covered with columnar epithelium, is found lining the alimentary canal below the cardiac orifice of the stomach, the biliary passages, the excretory ducts of all the glands, the nasal passages, the upper part of the pharynx, the uterus and Fallopian tubes, the bronchia, the Eustachian tubes and the male urethra. In certain situations this variety of epithelium is provided on its free surface with little hair-like processes called cilia. During life the cilia are in constant motion, producing a current generally in the direction of the mucous orifices. Ciliated epithelium is found throughout the nasal passages, beginning about three-quarters of an inch (19·1 mm.) within the nose; in the upper part of the pharynx; the posterior surface of the soft palate; the Eustachian tube; the tympanic cavity; the larynx, trachea, and bronchial tubes, until they become less than $\frac{1}{50}$ of an inch (0·5 mm.) in diameter; the neck and body of the uterus; the Fallopian tubes; the internal surface of the eyelids; and the ventricles of the brain. Mucous membranes of this variety are formed of a chorion, a basement-membrane and epithelium. The chorion is composed of inelastic and elastic fibres, a few non-striated muscular fibres, amorphous matter, blood-vessels, nerves and lymphatics. It is less dense and less elastic than the chorion of the first variety and generally is more closely united to the subjacent tissue. The surface of these membranes is generally smooth, the only exception being the mucous membrane of the pyloric portion of the stomach and the small intestines. These membranes are provided with follicular glands, extending through their entire thickness and terminating in rounded extremities, sometimes single and sometimes double, which rest upon the submucous structure. Many of them are provided also with simple racemose glands, the ducts passing through the membrane, and the glandular structure being situated in the submucous areolar tissue. The columnar epithelium covering these membranes rests upon an amorphous structure called basement-membrane. The epithelium generally presents but few layers, and sometimes, as in the intestinal canal, there is only a single layer. The cells are prismoidal, with a large, free extremity, and a pointed end which is attached. The cells of the lower strata are shorter and more rounded than those in the superficial layer. The cells are pale and very closely adherent to each other by their sides, each with a moderate-sized, oval nucleus and one or two nucleoli. The length of the cells is $\frac{1}{800}$ to $\frac{1}{600}$ of an inch (30 to 40 $\mu$), and their diameter, $\frac{1}{3000}$ to $\frac{1}{2500}$ of an inch (8 to 10 $\mu$). When villosities exist on the surface of the membranes, the cells follow the elevations and do not fill up the spaces between them, as in most of the membranes covered with squamous epithelium.

The mucous membrane of the urinary bladder, of the ureters and of the pelvis of the kidneys can not be classed in either of the above divisions. In these situations the membrane is covered with mixed epithelium, presenting all varieties of form between the squamous and the columnar, some of the cells being caudate and quite irregular in shape.

*Mechanism of the Secretion of Mucus.*—Nearly every one of the many fluids known under the name of mucus is composed of the products of several different glandular structures. Certain membranes which do not possess glands, as the mucous lining of the ureters and of a great portion of the urinary bladder, are capable of secreting mucus. The mucous membrane of the stomach produces an alkaline, viscid secretion, during the intervals of digestion, when the gastric glands do not act; and the gastric glands, during digestion, secrete a fluid of an entirely different character. The fluid produced by the follicles of the small intestine likewise has peculiar digestive properties. These considerations and the fact that the entire extent of the mucous membranes is covered with more or less secretion show that the general epithelial covering of these membranes is capable of secreting a fluid which forms one of the constituents of what is ordinarily recognized as mucus. It is impossible, however, to separate the secretion of the superficial layer of cells from the other fluids that are found on the mucous membranes; and it will be more convenient to regard as mucus, the secretion which is found upon mucous membranes, except when, as in the case of the gastric or the intestinal juice, a special fluid can be recognized by certain distinctive physiological properties.

In the membranes covered with columnar epithelium, which are usually provided with simple follicles, the secretion is produced mainly by these follicles, but in part by the epithelium covering the general surface. The membranes covered with squamous epithelium usually contain but few follicles and are provided with simple racemose glands situated in the submucous structure, which are to be regarded as appendages to the membrane. The secretion is here produced by the epithelium on the free surface and is always mixed with fluids resulting from the action of the mucous glands.

There is nothing to be said with regard to the mechanism of the secretion of mucus in addition to what has already been stated in connection with the general mechanism of secretion. All the mucous membranes are quite vascular, and the cells covering the membrane and lining the follicles and glands attached to it have the property of taking from the blood the materials necessary for the formation of the secretion. These matters pass out of the cells upon the surface of the membrane, in connection with water and inorganic salts in variable proportions. Many of the cells themselves are thrown off and are found in the secretion, together with a few leucocytes, which latter are produced upon mucous surfaces with great facility.

*Composition and Varieties of Mucus.*—All the varieties of mucus are more or less viscid; but this character is very variable in the secretions from different membranes, in some of them the secretion being quite fluid, and in others, almost semi-solid. The different kinds of mucus vary considerably in general appearance. Some of them are perfectly clear and colorless; but the secretion is generally grayish and semi-transparent. Examined by the microscope, in addition to the mixture of epithelium and the occasional leucocytes, which give to the fluid its semi-opaque character, the mass of the secretion presents a very finely striated appearance, as though it were composed of thin layers of nearly transparent substance with many folds. These delicate striæ do not usually interlace with each other, and they are rendered more distinct by the action of acetic acid. This appearance, with the peculiar effect of the acid, is characteristic of mucus. Some varieties of mucus present very fine, pale granulations and a few small globules of oil.

On the addition of water, mucus is somewhat swollen but is not dissolved. An exception to this is the secretion of the conjunctival mucous membrane, which is coagulated on the addition of water. As a rule the reaction of mucus is alkaline; the only exception to this being the vaginal mucus, which is very fluid and is distinctly acid.

It is difficult to get an exact idea of the composition of normal mucus, from the fact that the quantity secreted by the membranes in their natural condition is very small, being just sufficient to lubricate their surface. All varieties, however, contain a peculiar organic matter, called mucine, which gives to the fluid its peculiar viscidity. They likewise present a considerable variety of inorganic salts, as sodium chloride, potassium chloride, alkaline lactates, sodium carbonate, calcium phosphate, a small proportion of the sulphates, and in some varieties, traces of iron and of silica. Of all these constituents, mucine is the most important, as it gives to the secretion its characteristic properties. Like all other organic nitrogenized substances, mucine is coagulable by various reagents. It is imperfectly coagulated by heat; and after desiccation it can be made to assume its peculiar consistence by the addition of a small quantity of water. It is coagulated by acetic acid and by a small quantity of the strong mineral acids, being redissolved in an excess of the latter. It is also coagulated by strong alcohol, forming a fibrinous clot soluble in hot and cold water. Mucine may be readily isolated by adding water to a specimen of normal mucus, filtering, and precipitating with an excess of alcohol. If this precipitate, after having been dried, be exposed to water, it assumes the viscid consistence peculiar to mucine. This property serves to distinguish it from albumen and other organic nitrogenized matters.

*General Uses of Mucus.*—The smooth, viscid and adhesive character of mucus, forming, as this fluid does, a coating for the mucous membranes, serves to protect these parts, enables their surfaces to move freely one upon the other, and modifies to a certain extent the process of absorption. Aside from these mechanical uses, it has been shown that mucus, in connection with the epithelial covering of the mucous membranes, is capable of preventing the absorption of certain substances. It is well known, for example, that venoms may be applied with impunity to certain mucous surfaces, while they produce poisonous effects if introduced into the circulation. These agents are not neutralized by the secretions of the parts, for they will produce their characteristic effects upon the system when removed from the mucous surfaces and introduced into the circulation; and it is reasonable to suppose that the mucous membranes are capable of resisting their absorption. This fact is illustrated by the following experiment:

Let an endosmometer be constructed, using a fresh mucous membrane, on the surface of which the epithelium and layer of mucus remain intact, and in the interior of the apparatus, place a saccharine solution and let the membrane be exposed to a solution containing some venomous fluid. The liquid will mount in the interior of the apparatus, but the poison will not penetrate the membrane. If the mucus and epithelium be now removed with the finger-nail from even a small portion of the membrane, the poison will immediately pass through that part of the membrane, and an animal may be killed with the fluid which now penetrates into the interior of the endosmometer (Robin).

These facts show that mucus is an important secretion. It not only has a useful mechanical office, but it is in all probability closely connected with some of the phenomena of elective absorption which are so often observed, particularly in the alimentary canal.

*Physiological Anatomy of the Sebaceous, Ceruminous and Meibomian Glands.*—The true sebaceous glands are found in all parts of the skin that are provided with hair; and as nearly every part of the general surface presents either the long, the short or the downy hairs, these glands are very generally distributed. They exist, indeed, in greater or less numbers in all parts of the skin, except the palms of the hands and the soles of the feet. In the labia minora in the female, and in portions of the prepuce and glans penis of the male, parts not provided with hair, small, racemose sebaceous glands are found, which produce secretions differing somewhat from that formed by the ordinary glands. The glands in the areola of the nipple in the female are very large and are connected with small, downy hairs.

Nearly all of the sebaceous glands are either simple racemose glands, that is, presenting a number of follicles connected with a single excretory duct, or compound racemose glands, presenting several ducts, with their follicles, opening by a common tube. Although there is this variation in the size and arrangement of the glands of the general surface, they secrete essentially the same fluid, and their anatomical differences consist simply in a multiplication of follicles.

The differences in the size of the sebaceous glands bear a certain relation to the size of the hairs with which they are connected; and as a rule, the

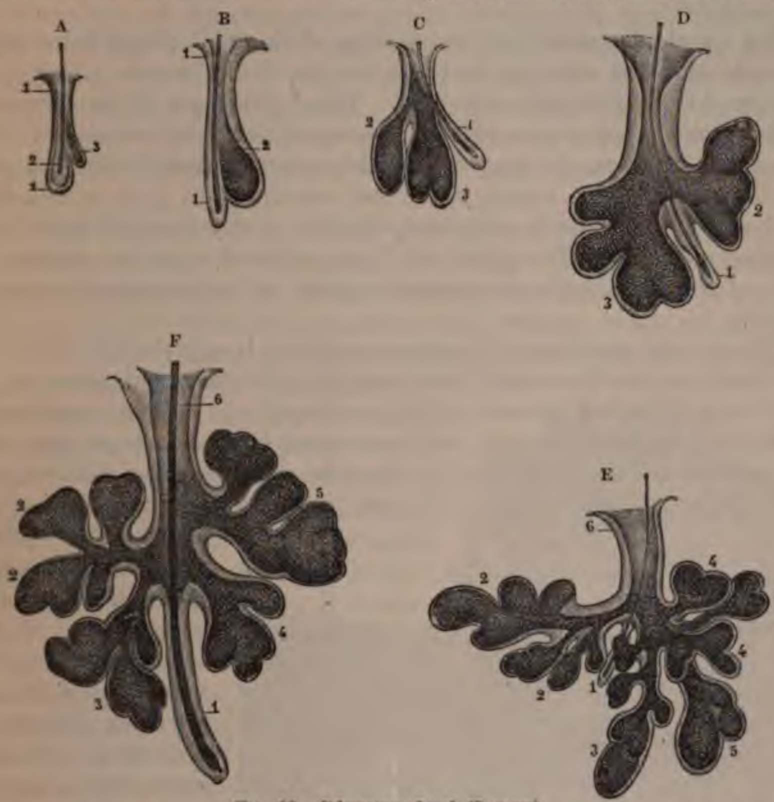


FIG. 99.—*Sebaceous glands* (Sappey).

A, a gland in its most rudimentary form: 1, rudimentary hair-follicle; 2, downy hair; 3, simple sebaceous follicle.
B, a gland more developed: 1, hair-follicle; 2, simple sebaceous follicle.
C, a gland with two follicles: 1, hair-follicle; 2, simple follicle; 3, follicle imperfectly divided.
D, a compound gland: 1, hair-follicle; 2, lobule with three follicles; 3, lobule with four follicles.
E, a gland with four lobules: 1, hair-follicle; 2, 2, first lobule; 3, second lobule; 4, 4, third lobule; 5, fourth lobule; 6, excretory duct with a hair passing through it.
F, a gland with four lobules: 1, hair-follicle; 2, 2, first lobule; 3, second lobule; 4, third lobule; 5, fourth lobule; 6, excretory duct.

largest glands are connected with the small, downy hairs. These distinctions in size are so marked, that the glands may be divided into two classes; viz., those connected with the long hairs of the head, face, chest, axilla and genital organs and with the coarse, short hairs, and those connected with the fine, downy hairs.

The glands connected with the larger hair-follicles are of the simple racemose variety and are $\frac{1}{120}$ to $\frac{1}{40}$ of an inch (0·21 to 0·64 mm.) in diameter. Two to five of these glands are generally found arranged around each hair-follicle. They discharge their secretion at about the junction of the upper third with the lower two-thirds of the hair-follicle. The follicles of the long hairs of the scalp are generally provided each with a pair of sebaceous glands, measuring $\frac{1}{120}$ to $\frac{1}{75}$ of an inch (0·21 to 0·34 mm.) in diameter. Encircling the hairs of the beard, the chest, axilla and genital organs, are large glands, some of them $\frac{1}{40}$ of an inch (0·64 mm.) in diameter, arranged in groups of four to eight.

The glands connected with the follicles of the small, downy hairs are so large, as compared with the hair-follicles, that the latter seem rather as appendages to the glandular structures. These glands are of the compound racemose variety and present sometimes as many as fifteen *culs-de-sac.* The largest are found on the nose, the ear, the curuncula lachrymalis, the penis and the areola of the nipple, where they measure $\frac{1}{50}$ to $\frac{1}{12}$ of an inch (0·51 to 2·1 mm.). The glands connected with the downy hairs of other parts usually are smaller. The glands of Tyson, situated upon the corona and cervix of the glans penis, are sebaceous glands of the compound racemose variety.

The minute structure of the sebaceous glands is very simple. The follicles which compose the simple glands and the follicular terminations of the simple and compound racemose glands are formed of a delicate, structureless or slightly granular membrane, with an external layer of inelastic and small elastic fibres, and are lined by cells. Next the membrane, the cells are polyhedric, pale and granular, most of them presenting a nucleus and a nucleolus; but the follicle itself contains fatty granules and the other constituents of the sebaceous matter, with cells filled with fatty particles. These cells abound in the sebaceous matter as it is discharged from the duct. The great quantity of fatty granules and globules found in the ducts and follicles of the sebaceous glands renders them dark and opaque when examined with the microscope by transmitted light, and their appearance is quite distinctive. The larger glands are surrounded with capillary blood-vessels.

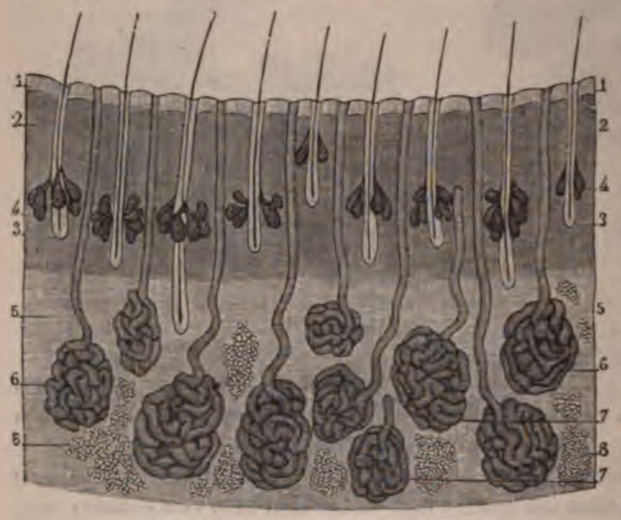

FIG. 100.—*Ceruminous glands* (Sappey).

Vertical section of the skin of the external auditory meatus: 1, 1, epidermis; 2, 2, derma; 3, 3, series of hair-follicles lodged in the substance of the skin; 4, 4, series of sebaceous glands attached to these follicles; 5, 5, subcutaneous areolar layer; 6, 6, ceruminous glands; 7, 7, ceruminous glands with the ducts divided; 8, 8, adipose vesicles.

The ceruminous glands produce a secretion resembling the sebaceous matter in many regards, but in their anatomy they are almost identical with the sudoriparous glands. They belong to the variety of glands called tubular, and they consist of a nearly straight tube which penetrates the skin, and a rounded or ovoid coil situated in the subcutaneous structure. These glands are found only in the cartilaginous portion of the external auditory meatus, where they exist in great numbers.

The ducts of the ceruminous glands are short and nearly straight, simply penetrating the different layers of the skin, and are $\frac{1}{700}$ to $\frac{1}{500}$ of an inch (36 to 50 $\mu$) in diameter. Their openings are rounded and about $\frac{1}{270}$ of an inch (93 $\mu$) in diameter. They sometimes terminate in the upper part of one of the hair-follicles. They present an external coat of fibrous tissue and are lined with several layers of small, pale, nucleated epithelial cells.

The glandular coil is an ovoid or rounded, brownish mass, $\frac{1}{120}$ to $\frac{1}{50}$ or $\frac{1}{16}$ of an inch (0·21 to 0·51 or 1·6 mm.) in diameter. It is simply a convoluted tube, continuous with the excretory duct and terminating in a somewhat dilated, rounded extremity. It occasionally presents small, lateral protrusions. The diameter of the tube is $\frac{1}{300}$ to $\frac{1}{250}$ of an inch (83 to 100 $\mu$). It has a fibrous coat, with a longitudinal layer of non-striated muscular fibres, and externally a few elastic fibres. It is lined by a single layer of irregularly polygonal cells, which are $\frac{1}{2000}$ to $\frac{1}{1250}$ of an inch (12 to 20 $\mu$) in diameter. These cells contain a number of brownish or yellowish pigmentary granules. The tube forming the gland contains a clear fluid mixed with a granular substance containing cells.

FIG. 101.—*Meibomian glands of the upper lid; magnified 7 diameters* (Sappey).

1, 1, free border of the lid; 2, 2, anterior lip penetrated by the eyelashes; 3, 3, posterior lip, with the openings of the Meibomian glands; 4, a gland passing obliquely at the summit; 5, another gland bent upon itself; 6, 6, two glands in the form of racemose glands at their origin; 7, a very small gland; 8, a medium-sized gland.

In addition to the ceruminous glands, sebaceous follicles are found connected with the hair-follicles. The arrangement of the ordinary sebaceous glands and the ceruminous glands, which are situated in different planes in the subcutaneous structure, is shown in Fig. 100.

The Meibomian glands have essentially the same structure as the ordinary sebaceous glands. Their ducts, however, are longer, and the terminal follicles are arranged in a peculiar manner by the sides of the tubes along their entire length. These glands are situated partly in the substance of the tarsal cartilages, between their posterior surfaces and the conjunctival mucous membrane. They are placed at right angles to the free border of the eyelids, opening upon the inner edge and occupying the entire width of the cartilages. Twenty-five to thirty glands are found in the upper lid, and twenty to twenty-five, in the lower lid.

Each Meibomian gland consists of a nearly straight excretory duct, $\frac{1}{307}$ to $\frac{1}{250}$ of an inch (83 to 100 $\mu$) in diameter, communicating laterally with compound racemose acini, or collections of follicles, measuring $\frac{1}{300}$ to $\frac{1}{125}$ of an inch (83 to 200 $\mu$). Fifteen or twenty of these collections of follicles are found on either side of the duct in glands of medium length. Most of the excretory ducts are nearly straight, but some are turned upon themselves near their upper extremity. The general arrangement of these glands is shown in Fig. 101.

In general structure there is little if any difference between the terminal follicles of the Meibomian glands and the follicles of the ordinary sebaceous glands. They are lined with cells $\frac{1}{2500}$ to $\frac{1}{1250}$ of an inch (10 to 20 $\mu$) in diameter. The cells contain fatty globules, but these do not coalesce into large drops, such as are often seen in the ordinary sebaceous cells. The follicles and ducts are filled with the whitish, oleaginous matter which constitutes the Meibomian secretion, or the sebum palpebrale.

In addition to the Meibomian secretion, the edges of the palpebral orifice receive a small quantity of secretion from ordinary sebaceous glands of the compound racemose variety (ciliary glands), which are appended in pairs to each of the follicles of the eyelashes, and from the sebaceous glands attached to the small hairs of the caruncula lachrymalis.

*Ordinary Sebaceous Matter.*—Although it may be inferred, from the great number of sebaceous glands opening upon the cutaneous surface, that the amount of sebaceous matter must be considerable, it has been impossible to collect the normal fluid in quantity sufficient for ultimate analysis. In some parts, as the skin of the nose, where the glands are particularly abundant, a certain quantity of oily secretion is sometimes observed, giving to the surface a greasy, glistening aspect. This may be absorbed by paper, giving it the well known appearance produced by oily matters, and it may be collected in small quantity upon a glass slide and examined microscopically. It then presents a number of strongly refracting fatty globules, with a few epithelial cells. The cells, however, are not abundant in the fluid as it is discharged upon the general surface; but if the contents of the ducts and follicles be examined, cells will here be found in great number. Most of the cells, indeed, remain in the glands, and the oily matter only is discharged. The object of this secretion is to lubricate the general cutaneous surface and to give to the hairs that softness which is characteristic of them when in a perfectly healthy condition.

The chemical constituents of the sebaceous matter are largely fatty. In an analysis made by Lutz, in a case of general hypertrophy of the sebaceous system, the proportion of water was only 357 parts per 1000. The solid matters consisted of oleine, 270 parts, palmitine, 135 parts, caseous matter, 129 parts, gelatine, 87 parts, a little albumen, butyric acid and sodium butyrate, with sodium phosphate, sodium chloride, sodium sulphate and traces of calcium phosphate. Cholesterine, which is present so frequently in the contents of sebaceous cysts, does not exist in the normal secretion.

During the later months of pregnancy and during lactation, the sebaceous glands of the areola of the nipple become considerably distended with a grayish-white, opaque secretion, containing oily globules and granules. Frequently the fluid contains also a large number of epithelial cells. During the periods above indicated, the secretion here is always much more abundant than in the ordinary sebaceous glands.

*Smegma of the Prepuce and of the Labia Minora.*—In the folds of the prepuce of the male and on the inner surface and folds of the labia minora in the female, a small quantity of a whitish, grumous matter, of a cheesy consistence, is sometimes found, particularly when proper attention is not paid to cleanliness. The matter which thus collects in the folds of the prepuce has really little analogy with the ordinary sebaceous secretion. Examination with the microscope shows that it is composed almost entirely of irregular scales of epithelium, which do not present the fatty granules and globules usually observed in the cells derived from the sebaceous glands. The production of this substance is probably independent of the secretion of sebaceous matter, as it is formed chiefly in parts of the prepuce in which the sebaceous glands are wanting.

The smegma of the labia minora is of the same character as the smegma preputiale; but it contains drops of oil and the other products of the sebaceous glands found in these parts.

*Vernix Caseosa.*—The surface of the fœtus at birth and near the end of uterogestation is generally covered with a whitish coating, or smegma, called the vernix caseosa. This is most abundant in the folds of the skin; but it usually covers the entire surface with a coating of greater or less thickness and of about the consistence of lard. There are great differences in fœtuses at term as regards the quantity of the vernix caseosa, In some the coating is so slight that it is observed only on close inspection. There are few analyses which give accurately the chemical composition of this substance; and the best idea of its constitution and mode of formation can be formed from microscopical examinations. If a small quantity be scraped from the surface and be spread out upon a glass slide with a little glycerine and water, it will be found on microscopical examination, to consist of a large number of epithelial cells with a very few small, fatty granules. These cells, after desiccation, constitute about ten per cent. of the entire mass. The fatty granulations are very few and do not seem to be necessary constituents of the vernix, as they are of the sebaceous matter. In fact, the vernix caseosa must be regarded as the residue of the secretion of the sebaceous glands, rather than an accumulation of true sebaceous matter.

The office of the vernix caseosa is undoubtedly protective. In making a microscopical preparation of the cells with water, it becomes evident that the coating is penetrated by the liquid with very great difficulty, even when mixed with it as thoroughly as possible. The protecting coat of vernix caseosa allows the skin to perform its office in utero, and at birth, when this coating is removed, the surface is found in a condition perfectly adapted to extraüterine existence. It is not probable that the vernix caseosa is necessary to facilitate the passage of the child into the world, for the parts of the mother are always sufficiently lubricated with mucous secretion.

*Cerumen.*—A peculiar substance of a waxy consistence is secreted by the glands that have been described in the external auditory meatus, under the name of ceruminous glands, mixed with the secretion of sebaceous glands connected with the short hairs in this situation. It is difficult to ascertain what share these two sets of glands have in the formation of the cerumen. According to Robin, the waxy portion of the secretion is produced entirely by the sebaceous glands, and the convoluted glands, commonly known as the ceruminous glands, produce a secretion like the perspiration. This view is to a certain extent reasonable; for the sebaceous matter is not removed from the meatus by friction, as in other situations, and would have a natural tendency to accumulate; but the contents of the ducts of the ceruminous glands differ materially from the fluid found in the ducts of the ordinary sudoriparous glands, containing granules and fatty globules such as exist in the cerumen. Although the glands of the ear are analogous in structure, and to a certain extent, in the character of their secretion, to the sudoriparous glands, the fluid which they produce is peculiar. The perspiratory glands of the axilla and of some other parts also produce secretions differing somewhat from ordinary perspiration. As far as can be ascertained, the cerumen is produced by both sets of glands. The sebaceous glands attached to the hair-follicles probably secrete most of the oleaginous and waxy matter, while the so-called ceruminous glands produce a secretion of much greater fluidity, but containing a certain quantity of granular and fatty matter.

The consistence and general appearance of cerumen are quite variable within the limits of health. When first secreted, it is of a yellowish color and about the consistence of honey, becoming darker and much more viscid upon exposure to the air. It has a very decided and bitter taste. It readily forms a sort of emulsive mixture with water.

Examined microscopically, the cerumen is found to contain semi-solid, dark granulations of an irregularly polyhedric shape, with epithelium from the sebaceous glands, and epidermic scales, both isolated and in layers. Sometimes, also, a few crystals of cholesterine are found.

Chemical examination shows that the cerumen is composed of oily matters fusible at a low temperature, a peculiar organic matter resembling mucine, with sodium salts and a certain quantity of calcium phosphate. The yellow coloring matter is soluble in alcohol; and the residue after evaporation of the alcohol is very soluble in water and may be precipitated from its watery solution by neutral lead acetate or tin chloride. This extract has a very bitter taste.

The cerumen lubricates the external meatus, accumulating in the canal around the hairs. Its peculiar bitter taste is supposed to be useful in preventing the entrance of insects.

*Meibomian Secretion.*—Very little is known concerning any special properties of the Meibomian fluid, except that it mixes in the form of an emulsion with water more readily than the other sebaceous secretions. It is produced in small quantity, mixed with mucus and the secretion from the ordinary sebaceous glands attached to the eyelashes and the glands of the caruncula lachrymalis, and smears the edges of the palpebral orifice. This oily coating on the edges of the lids, unless the tears be produced in excessive quantity, prevents their overflow upon the cheeks, and the excess of fluid passes into the nasal duct.

## MAMMARY SECRETION.

The mammary glands are among the most remarkable organs in the economy; not only on account of the peculiar character of their secretion, which is unlike the product of any other of the glands, but from the great changes which they undergo at different periods, both in size and structure. Rudimentary in early life and in the male at all periods of life, these organs are fully developed in the adult female only in the later months of pregnancy and during lactation. In the female, after puberty, the mammary glands undergo a marked and rapid increase in size; but even then they are not fully developed.

*Physiological Anatomy of the Mammary Glands.*—The form, size and situation of the mammæ in the adult female are too well known to demand more than a passing mention. These organs are almost invariably double and are situated on the anterior portion of the thorax, over the great pectoral muscles. In women who have never borne children, they generally are firm and nearly hemispherical, with the nipple at the most prominent point. In women who have borne children, the glands during the intervals of lactation usually are larger, are held more loosely to the subjacent parts and are often flabby and pendulous. The areola of the nipple, also, is darker.

In both sexes the mammary glands are nearly as fully developed at birth as at any time before puberty. They make their appearance at about the fourth month, in the form of little elevations of the structure of the true skin, which soon begin to send off processes beneath the skin, which are destined to be developed into the lobes of the glands. In the fœtus at term the glands measure hardly more than one-third of an inch (8·5 mm.) in diameter. At this time there are twelve to fifteen lobes in each gland, and each lobe is penetrated by a duct, with but few branches, composed of fibrous tissue and lined with cylindrical epithelium. The ends of these ducts are frequently somewhat dilated; but what have been called the gland-vesicles do not make their appearance before puberty. In the adult male the glands are half an inch to two inches (12·7 to 50·8 mm.) broad, and $\frac{1}{12}$ to $\frac{1}{4}$ of an inch (2·1 to 6·4 mm.) in thickness. In their structure, however, they present little if any difference from the rudimentary glands of the infant.

As the time of puberty approaches in the female, the rudimentary ducts of the different lobes become more and more ramified. Instead of each duct having but two or three branches, the different lobes, as the gland enlarges, are penetrated by innumerable ramifications which have gradually been developed as processes from the main duct. It is important to remember, however, that these branches are never so abundant or so long during the intervals of lactation as they are when the gland is in full activity.

Between the fourth and fifth months of uterogestation the mammary glands of the mother begin to increase in size; and at term they are very much larger than during the unimpregnated state. At this time the breasts become quite hard, and the surface near the areola is somewhat uneven, from the great development of the ducts. The nipple itself is increased in size, the papillæ upon its surface and upon the areola are more largely developed, and the areola becomes larger, darker and thicker. The glandular structure of the breasts during the latter half of pregnancy becomes so far developed, that if the child be born at the seventh month, the lacteal secretion may be established at the usual time after parturition. Even when parturition takes place at term, a few days elapse before secretion is fully established, and the first product of the glands, called colostrum, is very different from the fully formed milk.

The only parts of the covering of the breasts that present any peculiarities are the areola and the nipple. The surface of the nipple is covered with papillæ, which are very largely developed near the summit. It is covered by epithelium in several layers, the lower strata being filled with pigmentary granules. The true skin covering the nipples is composed of inelastic and elastic fibres, containing a large number of sebaceous glands, but no hair-follicles or sudoriparous glands. These glands are always of the racemose variety, and they never exist in the form of simple follicles (Sappey). The nipple contains the lactiferous ducts, fibres of inelastic and elastic tissue, with a large number of non-striated muscular fibres. The muscular fibres have no definite direction, but are so abundant that when they are contracted the nipple becomes very firm and hard.

The areola does not lie, like the general integument covering the gland, upon a bed of adipose tissue, but it is closely adherent to the subjacent glandular structure. The skin here is much thinner and more delicate than in other parts, and the pigmentary granules are very abundant in some of the lower strata of epidermic cells, particularly during pregnancy. The true skin of the areola is composed of inelastic and elastic fibres and lies upon a distinct layer of non-striated muscular fibres. The arrangement of the muscular fibres—sometimes called the subareolar muscle—is quite regular, forming concentric rings around the nipple. These fibres are supposed to be useful in compressing the ducts during the discharge of milk. The areolar presents the following structures; papillæ, considerably smaller than those upon the nipple; hair-follicles, containing small, rudimentary hairs; sudoriparous glands; and sebaceous glands connected with the hair-follicles. The sebaceous glands are very large, and their situation is indicated by little prominences on the surface of the areola, which are especially marked during pregnancy.

The mammary gland itself is of the compound racemose variety. It is covered in front by a subcutaneous layer of fat, and posteriorly it is enveloped in a fibrous membrane loosely attached to the pectoralis major muscle. A considerable quantity of adipose tissue is also found in the substance of the gland between the lobes.

Separated from the adipose and fibrous tissue, the mammary gland is found divided into lobes, fifteen to twenty-four in number. These are subdivided into lobules made up of a greater or less number of acini, or *culs-de-sac*. The secreting structure is of a reddish-yellow color and is distinctly granular, presenting a decided contrast to the pale and uniformly fibrous appearance of the gland during the intervals of lactation. If the ducts be injected from the nipple and be followed into the substance of the gland, each one will be found distributing its branches to a distinct lobe; so that the organ is really made up of a number of glands identical in structure.

The canals which discharge the milk at the nipple are called lactiferous or galactophorous ducts. They are ten to fourteen in number. The openings of the ducts at the nipple are very small, measuring only $\frac{1}{60}$ to $\frac{1}{40}$ of an inch (0·42 to 0·64 mm.). As each duct passes downward, it enlarges in the nipple to $\frac{1}{25}$ or $\frac{1}{12}$ of an inch (1 or 2 mm.) in diameter, and beneath the areola it presents an elongated dilatation, $\frac{1}{6}$ to $\frac{1}{3}$ of an inch (4·2 to 8·5 mm.) in diameter, called the sinus of the duct. During lactation a considerable quantity of milk collects in these sinuses, which serve as reservoirs. Beyond the sinuses, the caliber of the ducts measures $\frac{1}{12}$ to $\frac{1}{6}$ of an inch (2·1 to 4·2 mm.). The ducts penetrate the different lobes, branching and subdividing, to terminate finally in the collections of *culs-de-sac* which form the acini. There is no anastomosis between the different lactiferous ducts, and each one is distributed independently to one or more lobes.

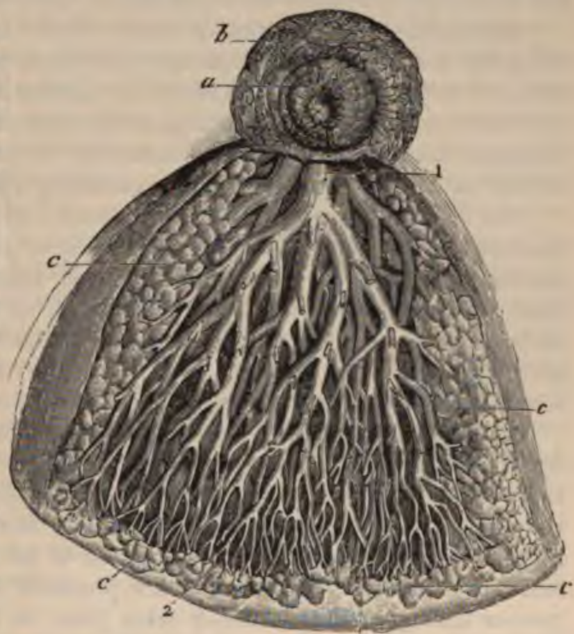


FIG. 102.—*Mammary gland of the human female* (Liégeois). *a*, nipple, the central portion of which is retracted; *b*, areola; *c*, *c*, *c*, *c*, lobules of the gland; 1, sinus, or dilated portion of one of the lactiferous ducts; 2, extremities of the lactiferous ducts.

The lactiferous ducts have three distinct coats. The external coat is composed of anastomosing fibres of elastic tissue with some inelastic fibres. The middle coat is composed of non-striated muscular fibres, arranged longitudinally and existing throughout the duct, from its opening at the nipple to the secreting *culs-de-sac*. The internal coat is an amorphous membrane, lined with flat, polygonal cells during the intervals of lactation and even during pregnancy, the cells being cylindrical in form and frequently presenting multiple nuclei, when milk is secreted.

The acini of the gland, which are very abundant, are visible to the naked eye, in the form of small, rounded granules of a reddish-yellow color. Between these acini, there exists a certain quantity of the ordinary white fibrous tissue, with quite a number of adipose vesicles. The presence of adipose tissue in considerable quantity in the substance of the glandular structure is peculiar to the mammary glands. Each acinus is made up of twenty to forty secreting vesicles. These vesicles are irregular in form, often varicose, and sometimes they are enlarged and imperfectly bifurcated at their terminal extremities. During lactation their diameter is $\frac{1}{400}$ to $\frac{1}{300}$ of an inch (60 to 80$\mu$).

During the intervals of lactation, as the lactiferous ducts become retracted, the glandular *culs-de-sac* disappear; and in pregnancy, as the gland takes on its full development, the ducts branch and extend themselves, and the vesicles are gradually developed around their extremities.

*Mechanism of the Secretion of Milk.*—With the exception of water and inorganic matters, all the important and characteristic constituents of the milk are formed in the substance of the mammary glands. The secreting structures have the property of separating from the blood a great variety of inorganic salts; and the milk furnishes all the inorganic matter necessary for the nutrition of the infant, even containing a small quantity of iron.

The lactose, or sugar of milk, the caseine, and the fatty particles, are all produced in the gland. The peculiar kind of sugar here found does not exist anywhere else in the organism. Even when the secretion of milk is most active, different varieties of sugar, such as glucose or cane-sugar, injected into the blood-vessels of a living animal, are never eliminated by the mammary glands, as they are by the kidneys; and their presence in the blood does not influence the quantity of lactose found in the milk.

Caseine is produced in the mammary glands, probably by a peculiar transformation of the albuminoid constituents of the blood. The fatty particles of the milk are likewise produced in the substance of the gland, and the peculiar kind of fat which exists in this secretion is not found in the blood. The mechanism of the production of fat in the mammary glands is somewhat obscure. The particles are produced in the cells, probably by a process analogous to that which takes place in the formation of the fatty particles found in the sebaceous matter.

As regards the mechanism of the formation of the peculiar and characteristic constituents of the milk, the mammary glands are to be classed among the organs of secretion and not with those of elimination or excretion; for none of these elements pre-exist in the blood, and they all appear first in the substance of the glands.

During the period of secretion, the glands receive a much larger supply of blood than at other times. Pregnancy favors the development of the secreting portions of the glands but does not induce secretion. On the other hand, when pregnancy occurs during lactation, it diminishes and modifies, and it may arrest the secretion of milk. The secreting action of the mammary glands is nearly continuous. When the secretion of milk has become fully established, while there may be certain times when it is formed in greater quantity than at others, there is no actual intermission in its production.

*General Conditions which modify the Lacteal Secretion.*—Very little is known concerning the physiological conditions which modify the secretion of milk. When lactation is fully established, the quantity and quality of the milk secreted become adapted to the requirements of the child at different periods of its existence. In studying the composition of the milk, therefore, it will be found to vary considerably in the different stages of lactation. It is evident that as the development of the child advances, a constant increase of nourishment is demanded; and as a rule, the mother is capable of supplying all the nutritive requirements of the infant for eight to twenty months.

During the time when such an amount of nutritive matter is furnished to the child, the quantity of food taken by the mother is sensibly increased; but observations have shown that the secretion of milk is not much influenced by the character of the food. It is necessary that the mother should be supplied with good, nutritious articles; but as far as solid food is concerned, there seems to be no great difference between a coarse and a delicate alimentation, and the milk of females in the lower walks of life, when the general condition is normal, is fully as good as in women who are able to live luxuriously. It is, indeed, a fact generally recognized by physiologists, that the secretion of milk is little influenced by any special diet, provided the alimentation be sufficient and of the quality ordinarily required by the system and that it contain none of the few articles of food which are known to have a special influence upon lactation. It is very common, however, for women to become quite fat during lactation; which shows that the fatty constituents of the food do not pass exclusively into the milk, but that there is a tendency, at the same time, to a deposition of adipose tissue in the situations in which it is ordinarily found. It is a matter of common experience, that certain articles, such as acids and fermentable substances, often disturb the digestive organs of the child without producing any change in the milk, that can be recognized by chemical analysis. The individual differences in women, in this regard, are very great.

The statements with regard to solid food do not apply to liquids. During lactation there is always an increased demand for water and for liquids generally; and if these be not supplied in sufficient quantity, the secretion of milk is diminished and its quality is almost always impaired. It is a curious fact, which has been fully established by observations upon the human subject and the inferior animals, that while the quantity of milk is increased by taking a large amount of simple water, the solid constituents are also increased, and the milk retains all of its qualities as a nutritive fluid.

Alcohol, especially when largely diluted, as in malt-liquors and other mild beverages, is well known to exert an influence upon the secretion of milk. Drinks of this kind almost always temporarily increase the activity of the secretion, and sometimes they produce a certain effect upon the child; but direct and accurate observations on the actual passage of alcohol into the milk are wanting. During lactation the moderate use of drinks containing a small proportion of alcohol is frequently beneficial, particularly in assisting the mother to sustain the unusual drain upon the system. There are, however, few instances of normal lactation in which their use is absolutely necessary.

It is well known that the secretion of milk may be profoundly affected by violent mental emotions. This is the case in many other secretions, as the saliva and the gastric juice. It is hardly necessary, however, to cite many instances of modification or arrest of the secretion from this cause, which are quoted by authors. Vernois and Becquerel reported a case, in which a hospital wet-nurse, who lost her only child from pneumonic fever, became violently affected with grief and presented, as a consequence, an immediate diminution in the quantity of her milk, with a great reduction in the proportion of salts, sugar and butter. In this case the proportion of caseine was increased. Astley Cooper reported two cases in which the secretion of milk was instantaneously and permanently arrested by terror. These cases are types of many others, which have been cited by writers, of the effects of mental emotions upon secretion.

Direct observations upon the influence of the nerves upon the mammary glands are few and unsatisfactory. The operation of dividing the nerves distributed to these glands, which has occasionally been practised upon animals in lactation, has not been observed to produce any sensible diminution in the quantity of the secretion. It is difficult, however, to operate upon all the nerves distributed to these organs. There are no observations indicating the situation of a nerve-centre presiding over the secretion of milk, although such a centre may exist.

*Quantity of Milk.*—It is difficult to form a reliable estimate of the average quantity of milk secreted by the human female in the twenty-four hours. The quantity undoubtedly varies very much in different persons; some women being able to nourish two children, while others, though apparently in perfect health, furnish hardly enough food for one. Astley Cooper, as the result of direct observation, stated that the quantity that can be drawn from a full breast is usually about two fluidounces (60 grammes). This may be assumed to be about the quantity contained in the lactiferous ducts when they are moderately distended. Lehmann, taking for the basis of his calculations the observations of Lampérierre, who found, as the result of sixty-seven experiments, that between 1·7 and 2 ounces (50 and 60 grammes) of milk were secreted in two hours, estimated that the average quantity discharged in twenty-four hours is about 44·5 fluidounces (1,320 grammes). Taking into consideration the variations in the quantity of milk secreted by different women, it may be assumed that the daily production is between two and three pints (950 and 1,420 grammes).

Certain conditions of the female are capable of materially influencing the quantity of milk secreted. It is evident that the secretion is usually somewhat increased within the first few months of lactation, when the progressive development of the child demands an increase in the quantity of nourishment. If the menstrual function become re-established during lactation, the milk usually is diminished in quantity during the periods, but sometimes it is not affected, either in its quantity or composition. Should the female become pregnant, there generally is a great diminution in the quantity of milk, and that which it secreted is ordinarily regarded as possessing little nutritive power. In obedience to a popular prejudice, apparently well founded, the child is usually taken from the breast as soon as pregnancy is recognized. No marked and constant variations have been observed in the quantity of milk in females of different ages.

*Properties and Composition of Milk.*—The general appearance and characters of ordinary cow's milk are sufficiently familiar. Human milk is neither so white nor so opaque as cow's milk, having ordinarily a slightly bluish tinge. After the secretion has become fully established, the fluid possesses no viscidity and is nearly opaque. It is almost inodorous, of a peculiar soft and sweetish taste, and when perfectly fresh it has a decidedly alkaline reaction. The taste of human milk is sweeter than that of cow's milk. A short time after its discharge from the gland, the reaction of milk becomes faintly acid; but this change takes place more slowly in human milk than in the milk of most of the inferior animals.

The average specific gravity of human milk is 1032; although this is subject to considerable variation, the minimum of eighty-nine observations being 1025, and the maximum, 1046 (Vernois and Becquerel). The observations of most physiological chemists have shown that this average is nearly correct.

Milk is not coagulated by heat, even after prolonged boiling; but a thin pellicle then forms on the surface, which is probably due to the combined action of heat and the atmosphere upon the caseine. Although a small quantity of albumen exists in the milk, this does not coagulate on the surface by the action of the heat, for the scum does not form when the fluid is heated in a vacuum or in an atmosphere of carbon dioxide or of hydrogen.

When the milk is coagulated by any substance acting upon the caseine or when it coagulates spontaneously it separates into a curd, composed of caseine with most of the fatty particles, and a nearly clear, greenish-yellow serum, called whey. This separation occurs spontaneously at a variable time after the discharge of the milk, taking place much sooner in warm than in cold weather. It is a curious fact that fresh milk frequently is coagulated during a thunder-storm, a phenomenon which has never been satisfactorily explained.

On being allowed to stand for a short time, the milk separates, without coagulating, into two tolerably distinct portions. A large proportion of the globules rises to the top, forming a yellowish-white and very opaque fluid, called cream, leaving the lower portion poorer in globules and of a decidedly bluish tint. In healthy milk the stratum of cream forms one-fifth to one-third of the entire mass of the milk. In the human subject the skim-milk is not white and opaque, but it is nearly as transparent as the whey. The specific gravity of the cream from milk of the average specific gravity of 1032 is about 1024. The specific gravity of skim-milk is about 1034.

*Microscopical Characters of the Milk.*—Milk contains an immense number of minute, spherical globules, of highly refractive power, held in suspension in a clear fluid. These are known under the name of milk-globules and are composed of palmitine, oleine, and fatty matters peculiar to milk.

The human milk-globules are $\frac{1}{25000}$ to $\frac{1}{1250}$ of an inch (1 to 20 $\mu$) in diameter. They usually are distinct from each other, but they may occasionally become collected into groups, without indicating any thing abnormal. In a perfectly normal condition of the glands, when the lacteal secretion has become fully established, the milk contains nothing but a clear fluid with these globules in suspension. The proportion of fatty matters in the milk is twenty-five to forty-eight parts per thousand; and this gives an idea of the proportion of globules which are seen on microscopical examination.

FIG. 103.—*Human milk-globules, from a healthy lying-in woman, eight days after delivery* (Funke).

In some regards milk does not present the characters of a simple emulsion. If it be shaken with ether, the mixture remains opaque; but the fatty matters are dissolved on the addition of potassium hydrate. Dilute acetic acid added to milk causes the globules to run together. These reactions have led to the view that the milk-globules have a membrane which is dissolved by potassium hydrate and by acetic acid. It is probable that the butter in normal milk does not exist precisely in the form of a simple emulsion, but that the globules have a very thin, caseous coating. In view of the action of reagents upon the globules, the only alternative, if the existence of a caseous coating be denied, is the opinion that the addition of potassium hydrate or of acetic acid renders the caseine incapable of holding the fat in the condition of an emulsion. There is actually little more than a verbal difference between these two opinions.

*Composition of the Milk.*—The following table, compiled by Robin from the analyses of various chemists, gives the constituents of human milk:

COMPOSITION OF HUMAN MILK.

| | | | |
|---|---|---|---|
| Water | 902·717 | to | 863·149 |
| Caseine (desiccated) | 29·000 | " | 39·000 |
| Lactoproteine | 1·000 | " | 2·770 |
| Albumen | traces | " | 0·880 |
| Butter, 25 to 38 — Palmitine | 17·000 | " | 25·840 |
| Butter, 25 to 38 — Oleine | 7·500 | " | 11·400 |
| Butter, 25 to 38 — Butyrine, caprine, caproïne, caprilene etc. | 0·500 | " | 0·760 |
| Sugar of milk (lactose) | 37·000 | " | 49·000 |
| Sodium lactate (?) | 0·420 | " | 0·450 |
| Sodium chloride | 0·240 | " | 0·340 |
| Potassium chloride | 1·440 | " | 1·830 |
| Sodium carbonate | 0·053 | " | 0·056 |
| Calcium carbonate | 0·069 | " | 0·070 |
| Calcium phosphate | 2·310 | " | 3·440 |
| Magnesium phosphate | 0·420 | " | 0·640 |
| Sodium phosphate | 0·225 | " | 0·230 |
| Ferric phosphate (?) | 0·032 | " | 0·070 |
| Sodium sulphate | 0·074 | " | 0·075 |
| Potassium sulphate | | traces. | |
| | 1,000·000 | | 1,000·000 |

Gases in solution { Oxygen ....... 1·29; Nitrogen ...... 12·17; Carbon dioxide. 16·54 } 30 parts per 1,000 in volume. (Hoppe.)

The proportion of water in milk is subject to certain changes, but these are not so considerable as might be expected from the great variations in the entire quantity of the secretion. As regards the quantity of milk in the twenty-four hours, the influence of drinks, even when nothing but pure water is taken, is very marked; and although the activity of the secretion is much increased by fluid ingesta, the quality of the milk usually is not affected, and the proportion of water to the solid matters remains about the same.

*Nitrogenized Constituents of Milk.*—Very little remains to be said concerning the nitrogenized constituents of human milk, after what has been stated in connection with alimentation. The different constituents of this class undoubtedly have the same nutritive office and they appear to be identical in all varieties of milk, the only difference being in their relative proportions. It is a matter of common experience, indeed, that the milk of many of the lower animals will take the place of human milk, when prepared so as to make the proportions of its different constituents approximate the composition of the natural food of the child. A comparison of the composition of human milk and of cow's milk shows that the former is poorer in nitrogenized matters and richer in butter and sugar; and consequently, the upper strata of cow's milk, properly sweetened and diluted with water, very nearly represents the ordinary breast-milk.

Caseine is by far the most important of the nitrogenized constituents of milk, and it supplies nearly all of this kind of nutritive matter demanded by the child. Lactoproteine, described by Millon and Commaille, is not so well defined, and albumen exists in the milk in very small quantity.

The coagulation of milk depends upon the reduction of caseine from a liquid to a semi-solid condition. When milk is allowed to coagulate spontaneously, the change is effected by the action of the lactic acid which results from a transformation of a portion of the sugar of milk. Caseine, in fact, is coagulated by any of the acids, even the feeble acids of organic origin. It differs from albumen in this regard and in the fact that it is not coagulated by heat. If fresh milk be slightly raised in temperature and be treated with an infusion of the gastric mucous membrane of the calf, coagulation will take place in five or ten minutes, the clear liquid still retaining its alkaline reaction. Simon has observed that the mucous membrane of the stomach of an infant a few days old, that had recently died, coagulated woman's milk more readily than the mucous membrane of the stomach of the calf.

*Non-Nitrogenized Constituents of Milk.*—Non-nitrogenized matters exist in abundance in the milk. The liquid caseine and the water hold the fats in the condition of a fine and permanent emulsion. This fat may easily be separated from the milk, and is known under the name of butter. In human milk, the butter is much softer than in the milk of many of the inferior animals, particularly the cow; but it is composed of essentially the same constituents, although in different proportions. In different animals, there are developed, even after the discharge of the milk, certain odorous matters, which are more or less characteristic of the animal from which the butter is taken.

The greatest part of the butter consists of palmitine. Butter contains in addition, oleine, and a small proportion of peculiar fats, which have not been very well determined, called butyrine, caprine, caproïne, capriline, with some other analogous substances. Palmitine and oleine are found in the fat throughout the body; but the last-named substances are peculiar to the milk. These are especially liable to acidification, and the acids resulting from their decomposition give the peculiar odor and flavor to rancid butter.

Sugar of milk, or lactose, is the most abundant of the solid constituents of the mammary secretion. It is this that gives to the milk its peculiar sweetish taste, although this variety of sugar is much less sweet than cane-sugar. The chief peculiarities of milk-sugar are that it readily undergoes change into lactic acid in the presence of nitrogenized ferments, and that it takes on alcoholic fermentation slowly and with difficulty. In the fermentation of milk, the lactose is changed first into galactose, and then into alcohol and carbon dioxide. In some parts of the world, alcoholic beverages made from milk are in common use.

*Inorganic Constituents of Milk.*—It is probable that many inorganic salts exist in the milk, which are not given in the table; and the separation of these from their combinations with organic matters is one of the most difficult problems in physiological chemistry. This must be the case, for during the first months of extraüterine existence, the child derives all the inorganic as well as the organic matters necessary to nutrition and development, from the breast of the mother. The reaction of the milk depends upon the presence of the alkaline carbonates, and these are important in preserving the fluidity of the caseine. It is not determined precisely in what form iron exists in the milk, but its presence here is undoubted. A comparison of the composition of the milk with that of the blood shows that most of the important inorganic matters found in the latter fluid exist also in the milk.

Hoppe has indicated the presence of carbon dioxide, nitrogen and oxygen, in solution in milk. Of these gases, carbon dioxide is the most abundant. It is well known that the presence of gases in solution in liquids renders them more agreeable to the taste, and carbon dioxide increases very materially their solvent properties. Aside from these considerations, the uses of the gaseous constituents of the milk are not apparent.

In addition to the constituents given in the table of composition, the milk contains small quantities of peptone, nucleine, dextrine, urea, lecithine, hypoxanthine, fluorine and silica.

A study of the composition of the milk fully confirms the fact that this is a typical alimentary fluid and presents in itself the proper proportion and variety of material for the nourishment of the body during the period when the development of the system is going on with its maximum of activity. The form in which its different nutritive constituents exist is such that they are easily digested and are assimilated with great rapidity.

*Variations in the Composition of Milk.*—If the composition of the milk be compared at different periods of lactation, it will be found to undergo great changes during the first few days. In fact, the first fluid secreted after parturition is so different from ordinary milk, that it has been called by another name. It is then known as colostrum, the peculiar properties of which will be considered more fully under a distinct head. As the secretion of milk becomes established, the fluid, from the first to the fifteenth day, becomes gradually diminished in density and in its proportion of water and of sugar, while there is a progressive increase in the proportion of most of the other constituents; viz., butter, caseine and the inorganic salts. The milk, therefore, as far as one can judge from its composition, as it increases in quantity during the first few days of lactation, is constantly increasing in its nutritive properties.

The differences in the composition of the milk, taken from month to month during the entire period of lactation, are not so distinctly marked. It is difficult, indeed, to indicate any constant variations of sufficient importance to lead to the view that the milk varies much in its nutritive properties at different times, during the ordinary period of lactation. The differences between the milk of primiparæ and multiparæ are slight and unimportant. As a rule, however, the milk of primiparæ approaches more nearly the normal standard.

In normal lactation, there is no marked and constant difference in composition between milk that has been secreted in great abundance and milk which is produced in comparatively small quantity; and the difference between the fluid first drawn from the breast and that taken when the ducts are nearly empty, which is observed in the milk of the cow, has not been noted in human milk.

### COLOSTRUM.

Near the end of uterogestation, during a period which varies considerably in different women and has not been accurately determined, a small quantity of a thickish, stringy fluid may frequently be drawn from the mammary glands. This bears little resemblance to perfectly formed milk. It is small in quantity and is usually more abundant in multiparæ than in primiparæ. This fluid, as well as that secreted for the first few days after delivery, is called colostrum. It is yellowish, semi-opaque, of a distinctly alkaline reaction and is somewhat mucilaginous in its consistence. Its specific gravity is considerably above that of the ordinary milk, being between 1040 and 1060. As lactation progresses, the character of the secretion rapidly changes, until the fluid becomes filled with true milk-globules and assumes the characters of ordinary milk.

The opacity of the colostrum is due to the presence of a number of different corpuscular elements. Milk-globules, very variable in size and number, are to be found in the secretion from the first. These, however, do not exist in sufficient quantity to render the fluid very opaque, and they are frequently aggregated in rounded and irregular masses, held together, apparently, by some glutinous matter. Peculiar corpuscles, supposed to be characteristic of the colostrum, always exist in this fluid. These are known as colostrum-corpuscles. They are spherical, varying in size between $\frac{1}{2500}$ and $\frac{1}{500}$ of an inch (10 and 50 $\mu$.), are sometimes pale, but more frequently quite granular, and they contain very often a large number of fatty particles. They behave in all respects like leucocytes and are described as a variety of these bodies. Many of them are precisely like the leucocytes found in the blood, lymph or pus. In addition to these corpuscular elements, a small quantity of mucine may frequently be observed in the colostrum on microscopical examination.

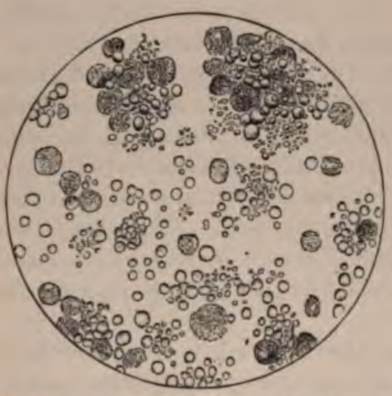

FIG. 104.—*Colostrum, from a healthy lying-in woman, twelve hours after delivery* (Funke).
The smaller globules are globules of milk. The larger globules, *a*, *a*, filled with granulations, are colostrum-corpuscles. As lactation advances, the colostrum-corpuscles gradually disappear, and the milk-globules become more abundant, smaller and more nearly uniform in size.

On the addition of ether to a specimen of colostrum under the microscope, most of the fatty particles, both within and without the colostrum-corpuscles, are dissolved. Ammonia added to the fluid renders it stringy, and sometimes the entire mass assumes a gelatinous consistence.

In its composition, colostrum presents many points of difference from true milk. It is sweeter to the taste and contains a greater proportion of sugar and of the inorganic salts. The proportion of fat is at least equal to the proportion in the milk and is generally greater. Instead of caseine, pure colostrum contains a large proportion of serum-albumen; and as the character of the secretion changes in the process of lactation, the albumen becomes gradually reduced in quantity and caseine takes its place.

The following, deduced from the analyses of Clemm, may be taken as the ordinary composition of colostrum of the human female:

COMPOSITION OF COLOSTRUM.

| | |
|---|---|
| Water | 945·24 |
| Albumen, and salts insoluble in alcohol | 29·81 |
| Butter | 7·07 |
| Sugar of milk, extractive matter, and salts soluble in alcohol | 17·27 |
| Loss | 0·61 |
| | 1,000·00 |

Colostrum ordinarily decomposes much more readily than milk and takes on putrefactive changes very rapidly. If it be allowed to stand for twelve to twenty-four hours, it separates into a thick, opaque, yellowish cream and a serous fluid. In an observation by Astley Cooper, nine measures of colostrum, taken soon after parturition, after twenty-four hours of repose, gave six parts of cream to three of milk.

The peculiar constitution of the colostrum, particularly the presence of an excess of sugar and inorganic salts, renders it somewhat laxative in its effects, and it is supposed to be useful, during the first few days after delivery, in assisting to relieve the infant of the accumulation of meconium.

As the quantity of colostrum that may be pressed from the mammary glands during the latter periods of utero-gestation, particularly the last month, is very variable, it becomes an important question to determine whether this secretion have any relation to the quantity of milk that may be expected after delivery. This question has been studied by Donné, who arrived at the following conclusions:

In women in whom the secretion of colostrum is almost absent, the fluid being in exceedingly small quantity, viscid, and containing hardly any corpuscular elements, there is hardly any milk produced after delivery.

In women who, before delivery, present a moderate quantity of colostrum, containing very few milk-globules and a number of colostrum-corpuscles, after delivery the milk will be scanty or it may be abundant, but it is always of poor quality.

When the quantity of colostrum produced is considerable, the secretion being quite fluid and rich in corpuscular elements, particularly milk-globules, the milk after delivery is always abundant and of good quality.

From these observations, it would seem that the production of colostrum is an indication of the proper development of the mammary glands; and the early production of fatty granules, which are first formed by the cells lining the secreting vesicles, indicates the probable activity in the secretion of milk after lactation shall have become fully established.

The secretion of the mammary glands preserves the characters of colostrum until toward the end of the so-called milk-fever, when the colostrum-corpuscles rapidly disappear, and the milk-globules become more abundant, regular and uniform in size. It may be stated, in general terms, that the secretion of milk becomes fully established and all the characters of the colostrum disappear between the eighth and the tenth day after delivery. A few colostrum-corpuscles and masses of agglutinated milk-globules may sometimes be discovered after the tenth day, but they are rare. After the fifteenth day, the milk does not sensibly change in its microscopical or its chemical characters.

## Lacteal Secretion in the Newly-Born.

In infants of both sexes there is generally a certain amount of secretion from the mammary glands, beginning at birth or two or three days after, and continuing sometimes for two or three weeks. The quantity of fluid that may be pressed out at the nipples at this time is very variable. Sometimes only a few drops can be obtained, but occasionally the fluid amounts to one or two drachms (3·7 or 7·4 grammes.) Although it is impossible to indicate the object of this secretion, which takes place when the glands are in a rudimentary condition, it has been so often observed and described by physiologists, that there can be no doubt with regard to the nature of the fluid and the fact that the secretion is almost always produced in greater or less quantity. The following is an analysis by Quevenne of the secretion obtained by Gubler. The observations of Gubler were made upon about twelve hundred children. The secretion rarely continued for more than four weeks, but in four instances it persisted for two months.

COMPOSITION OF THE MILK OF THE INFANT.

| | |
|---|---|
| Water | 894·00 |
| Caseine | 26·40 |
| Sugar of milk | 62.20 |
| Butter | 14·00 |
| Earthy phosphates | 1·20 |
| Soluble salts (with a small quantity of insoluble phosphates) | 2·20 |
| | 1,000·00 |

This fluid does not differ much in its composition from ordinary milk. The proportion of butter is much less, but the proportion of sugar is greater, and the quantity of caseine is nearly the same.

Of the other fluids which are enumerated in the list of secretions, the saliva, gastric juice, pancreatic juice and the intestinal fluids have already been described in connection with the physiology of digestion. The physiology of the lachrymal secretion will be taken up in connection with the eye, and the bile will be treated of fully under the head of excretion.

*Secretory Nerve-Centres.*—It remains now to consider the influence of nerve-centres upon certain secretions. Cerebro-spinal centres presiding over secretion have not been determined for all of the glands, although they may exist. No cerebro-spinal centres have been described for the secretions of mucous membranes, the gastric juice, the intestinal juice, the sebaceous fluids, the milk or the lachrymal fluid.

The centres for the salivary secretions are in the medulla oblongata, near the points of origin of the facial and glosso-pharyngeal nerves. The centre for the pancreatic secretion is also in the medulla oblongata. The centres which act upon the liver and upon certain excretions will be treated of in connection with the physiology of the liver, kidneys and skin.

## CHAPTER XII.

### *EXCRETION BY THE SKIN AND KIDNEYS.*

Differences between the secretions proper and the excretions—Physiological anatomy of the skin—Physiological anatomy of the nails—Physiological anatomy of the hairs—Sudden blanching of the hair—Perspiration—Sudoriparous glands—Mechanism of the secretion of sweat—Properties and composition of the sweat—Peculiarities of the sweat in certain parts—Physiological anatomy of the kidneys—Mechanism of the production and discharge of urine—Influence of blood-pressure, the nervous system etc., upon the secretion of urine—Physiological anatomy of the urinary passages—Mechanism of the discharge of urine—Properties and composition of the urine—Influence of ingesta upon the composition of the urine and upon the elimination of nitrogen—Influence of muscular exercise upon the elimination of nitrogen—Water regarded as a product of excretion—Variations in the composition of the urine.

In entering upon the study of the elimination of effete matters, it is necessary to appreciate fully the distinctions between the secretions proper and the excretions, in their composition, the mechanism of their production, and their destination. The urine may be taken as the type of the excrementitious fluids. None of its normal constituents belong to the class of non-crystallizable, organic nitrogenized matters, but it is composed entirely of crystallizable matters, simply held in solution in water. The solid constituents of the urine represent the ultimate physiological changes of certain parts of the organism, and they are in such a condition that they are of no farther use in the economy and are simply discharged from the body. Certain inorganic matters are found in the excrementitious fluids, are discharged with the products of excretion, and are thus associated with the organic constituents of the body in their physiological changes as well as in their deposition in the tissues. Coagulable organic matters, or albuminoids, never exist in the excrementitious fluids under normal conditions; except as the products of other glands may become accidentally or constantly mixed with the excrementitious fluids proper. The same remark applies to the non-nitrogenized matters, sugars and fats, which, whether formed in the organism or taken as food, are consumed in the organism. The production of the excretions is constant, being subject only to certain modifications in activity, which are dependent upon varying conditions of the system. All of the elements of excretion pre-exist in the blood, either in the condition in which they are discharged or in some slightly modified form.

The urine is a purely excrementitious fluid. The perspiration and the secretion of the axillary glands are excrementitious fluids, but they contain a certain quantity of the secretion of the sebaceous glands. Certain excrementitious matters are found in the bile, but at the same time, this fluid contains substances that are formed in the liver, and it has an important office as a secretion, in connection with the processes of digestion.

## Physiological Anatomy of the Skin.

The skin is one of the most complex and important structures in the body, and it has a variety of uses. In the first place, it forms a protective covering for the general surface. It is quite thick over the parts most subject to pressure and friction, is elastic over movable parts and those liable to variations in size, and in many situations, is covered with hair, which affords an additional protection to the subjacent structures. The skin and its appendages are imperfect conductors of caloric, are capable of resisting very considerable variations in temperature, and they thus tend to maintain the normal standard of the animal heat. As an organ of sensibility, the skin has important uses, being abundantly supplied with sensory nerves, some of which present an arrangement peculiarly adapted to the nice appreciation of tactile impressions. The skin assists in preserving the external forms of the muscles. It also relieves the abrupt projections and depressions of the general surface and gives roundness and grace to the contours of the body. In some parts it is very closely attached to the subjacent structures, while in others it is less adherent and is provided with a layer of adipose tissue.

As an organ of excretion, the skin is very important; and although the quantity of excrementitious matter exhaled from it is not very great, the evaporation of water from the general surface is always considerable and is subject to such modifications as may become necessary from the varied conditions of the animal temperature. Thus, while the skin protects the body from external influences, its office is important in regulating the heat produced as one of the phenomena attendant upon the general process of nutrition.

As the skin presents such a variety of uses, its physiological anatomy is most conveniently considered in connection with different divisions of the subject of physiology. For example, under the head of secretion, the structure of the different varieties of sebaceous glands has already been described; and the anatomy of the skin as an organ of touch will be most appropriately considered in connection with the physiology of the nervous system. In connection with the excreting organs found in the skin, it will be convenient to describe briefly its general structure and the most important points in the anatomy of the epidermic appendages. A full and connected description of the skin and its appendages belongs properly to works upon anatomy.

*Extent and Thickness of the Skin.*—Sappey has made a number of observations upon the extent of the surface of the skin. Without detailing the measurements of different parts, it may be stated, as the general result of his observations, that the cutaneous surface in a good-sized man is equal to a little more than sixteen square feet (15,000 square centimetres); and in men of more than ordinary size, it may extend to twenty-one or twenty-two square feet (2 square metres). In women of medium size, as the mean result of three observations, the surface was found to equal about twelve and a half square feet (11,500 square centimetres).

The thickness of the skin varies very much in different parts. Where it is exposed to constant pressure and friction, as on the soles of the feet or the palms of the hands, the epidermis becomes very much thickened, and in this way the more delicate structure of the true skin is protected. It is well known that the development of the epidermis, under these conditions, varies in different persons, with the pressure and friction to which the surface is habitually subjected. The true skin is $\frac{1}{12}$ to $\frac{1}{8}$ of an inch (2·1 to 3·2 mm.) in thickness; but in certain parts, particularly in the external auditory meatus, the lips and the glans penis, it frequently measures not more than $\frac{1}{100}$ of an inch (0·254 mm.).

*Layers of the Skin.*—The skin is naturally divided into two principal layers, which may be readily separated from each other by maceration. These are the true skin—cutis vera, derma, or corium—and the epidermis, cuticle, or scarf-skin. The true skin is more or less closely attached to the subjacent structures by a fibrous structure called the subcutaneous areolar tissue, in the meshes of which there is usually a certain quantity of adipose tissue. This layer is sometimes described under the name of the panniculus adiposus. The thickness of the adipose layer varies very much in different parts of the general surface and in different persons. There is no fat beneath the skin of the eyelids, the upper and outer part of the ear, the penis and the scrotum. Beneath the skin of the cranium, the nose, the neck, the dorsum of the hand and foot, the knee and the elbow, the fatty layer is about $\frac{1}{12}$ of an inch (2·1 mm.) in thickness. In other parts it usually measures $\frac{1}{6}$ to $\frac{1}{2}$ of an inch (4·2 to 12·7 mm.). In very fat persons it may measure an inch (25·4 mm.) or more. Upon the head and the neck, in the human subject, are muscles attached more or less closely to the skin. These are capable of moving the skin to a slight extent. Muscles of this kind are largely developed and quite extensively distributed in some of the lower animals.

There is no sharply defined line of demarcation between the cutis and the subcutaneous areolar tissue; and the under surface of the skin is always irregular, from the presence of fibres which are necessarily divided in detaching it from the subjacent structures. The fibres which enter into the composition of the skin become looser in their arrangement near its under surface, the change taking place rather abruptly, until they present large alveoli, which generally contain a certain quantity of adipose tissue.

The layer called the true skin is subdivided into a deep, reticulated or fibrous layer, and a superficial portion, called the papillary layer. The epidermis is also divided into two layers, as follows: an external layer, called the horny layer; and an internal layer, called the Malpighian, or the mucous layer, which is in contact with the papillary layer of the corium.

*The Corium, or True Skin.*—The reticulated and the papillary layers of the true skin are quite distinct. The lower stratum, the reticulated layer, is much thicker than the papillary layer and is dense, resisting, quite elastic and slightly contractile. It is composed of bundles of fibrous tissue, interlacing with each other in every direction, generally at acute angles. Distributed throughout this layer, are found anastomosing elastic fibres of the small variety, and with them a number of non-striated muscular fibres. This portion of the skin contains, in addition, a considerable quantity of amorphous matter, which serves to hold the fibres together. The muscular fibres are particularly abundant about the hair-follicles and the sebaceous glands connected with them, and their arrangement is such that when they are excited to contraction by cold or by electricity, the follicles are drawn up, projecting upon the general surface and producing the appearance known as "goose-flesh." Contraction of these fibres is particularly marked about the nipple, producing the so-called erection of this organ, and about the scrotum and penis, wrinkling the skin of these parts. The peculiar arrangement of the little muscles around the hair-follicles, forming little bands attached to the surface of the true skin and the base of the follicles, explains fully the manner in which the "goose-flesh" is produced. (See Fig. 107, page 349.) Contraction of the skin, under the stimulus of electricity, has been repeatedly demonstrated, both in the living subject and in executed criminals immediately after death.

The papillary layer of the skin passes insensibly into the subjacent structure without any marked line of division. It is composed chiefly of amorphous matter like that which exists in the reticulated layer. The papillæ themselves appear to be simple elevations of this amorphous matter, although they contain a few fibres, connective-tissue nuclei and little corpuscular bodies called cytoblastions (Robin).

As regards their form, the papillæ may be divided into two varieties; the simple and the compound. The simple papillæ are conical, rounded or club-shaped elevations of the amorphous matter and are irregularly distributed on the general surface. The smallest are $\frac{1}{700}$ to $\frac{1}{400}$ of an inch (36 to 62 $\mu$) in length and are found chiefly upon the face. The largest are on the palms of the hands, the soles of the feet, and the nipple. These measure $\frac{1}{250}$ to $\frac{1}{200}$ of an inch (100 to 125 $\mu$). Large papillæ, regularly arranged in a longitudinal direction, are found beneath the nails. The regular, curved lines observed upon the palms of the hands and the soles of the feet, particularly the palmar surfaces of the last phalanges, are formed by double rows of compound papillæ, which present two, three or four elevations attached to a single base. In the centre of each of these double rows of papillæ, is a fine and shallow groove, in which are found the orifices of the sudoriferous ducts.

The papillæ are abundantly supplied with blood-vessels terminating in looped capillary plexuses and with nerves. The termination of the nerves is peculiar and will be fully described in connection with the organs of touch. The arrangement of the lymphatics, which are very abundant in the skin, has already been indicated in the general description of the lymphatic system.

*The Epidermis and its Appendages.*—The epidermis, or external layer of the skin, is composed of cells. It has neither blood-vessels, nerves nor lymphatics. Its external surface is marked by shallow grooves, which correspond to the deep furrows between the papillæ of the derma. Its internal surface is applied directly to the papillary layer of the true skin and follows closely all its inequalities. This portion of the skin is subdivided into two tolerably distinct layers. The internal layer is called the rete mucosum, or the Malpighian layer, and the external is called the horny layer. These two layers present certain important distinctive characters.

The Malpighian layer is composed of a single stratum of prismoidal, nucleated cells, containing pigmentary matter, which are applied directly to all the inequalities of the derma, and of a number of layers of rounded cells containing no pigment. The upper layers of cells, with the scales of the horny layer, are semi-transparent and nearly colorless; and it is the pigmentary layer chiefly which gives to the skin its characteristic color and the peculiarities in the complexion of different races and of different individuals. All the epidermic cells are somewhat colored in the dark races, but the upper layers contain no pigmentary granules. The thickness of the rete mucosum is $\frac{1}{1700}$ to $\frac{1}{75}$ of an inch (15 to 333 $\mu$).

The horny layer is composed of a number of strata of hard, flattened cells, irregularly polygonal in shape and generally without nuclei. The deeper cells are thicker and more rounded than those of the superficial layers.

The epidermis serves as a protection to the more delicate structure of the true skin, and its thickness is in proportion to the exposure of the different parts. It is consequently much thicker upon the soles of the feet and the palms of the hands than in other portions of the general surface, and its thickness is very much increased in those who are habitually engaged in manual labor. Upon the face and eyelids, and in the external auditory passages, the epidermis is most delicate. The variations in thickness depend entirely upon the development of the horny layer. The thickness of the rete mucosum, although it varies in different parts, is rather more uniform.

There is constantly more or less desquamation of the epidermis, particularly of the horny layer, and the cells are regenerated from the subjacent parts. It is probable that there is a constant formation of cells in the deeper strata of the horny layer, which become flattened as they near the surface; but there is no direct evidence that the cells of the rete mucosum undergo transformation into the hard, flattened scales of the horny layer.

*Physiological Anatomy of the Nails.*—The nails are situated on the dorsal surfaces of the distal phalanges of the fingers and toes. They serve to protect these parts, and in the fingers, they are quite important in prehension. The general appearance of the nails is sufficiently familiar. In their description, anatomists have distinguished a root, a body and a free border.

The root of the nail is thin and soft, terminating in rather a jagged edge, which is turned slightly upward and is received into a fold of the skin, extending around the nail to its free edge. The length of the root varies with the size of the nail, but it is generally one-fourth to one-third of the length of the body.

The body of the nail extends from the fold of skin which covers the root, to the free border. This portion of the nail, with the root, is closely adherent by its under surface to the true skin. It is marked by fine but distinct longitudinal striæ and very faint transverse lines. It usually is reddish in color on account of the great vascularity of the subjacent structure. At the posterior part, is a whitish portion, of a semilunar shape, called the lunula, which has this appearance simply from the fact that the corium in this part is less vascular and the papillæ are not so regular as in the rest of the body. That portion of the skin situated beneath the root and the body of the nail is called the matrix. It presents highly vascular papillæ, arranged in regular, longitudinal rows, and it receives into its grooves corresponding ridges on the under surface of the nail.


FIG. 105 —*Anatomy of the nails* (Sappey).

A, nail *in situ*: 1, cutaneous fold covering the root of the nail; 2, section of this fold, turned back to show the root of the nail; 3, lunula; 4, nail.
B, concave or adherent surface of the nail: 1, border of the root; 2, lunula and root; 3, body; 4, free border.
C, longitudinal section of the nail: 1, 2, epidermis; 3, superficial layer of the nail; 4, epidermis of the pulp of the finger; 5, 6, true skin; 7, 11, bed of the nail; 8, Malpighian layer of the pulp of the finger; 9, 10, true skin on the dorsal surface of the finger; 12, true skin of the pulp of the finger; 13, last phalanx of the finger.

The free border of the nail begins where the nail becomes detached from the skin. This is generally cut or worn away and is constantly growing; but if left to itself, it attains in time a definite length, which may be stated, in general terms, to be an inch and a half to two inches (40 to 50 mm.).

On examining the nail in a longitudinal section, the horny layer, which is usually regarded as the true nail, is found to increase progressively in thickness from the root to near the free border. If the nail be examined in a transverse section, it will also be found much thicker in the central portion than near the edge, and that part which is received into the lateral portions of the fold becomes excessively thin like the rest of the root. The nail becomes somewhat thinner at and near the free border.

Sections of the nails show that they are composed of two layers, which correspond to the Malpighian and the horny layers of the epidermis, although they are much more distinct. The Malpighian layer is applied directly to the ridges of the bed of the nail and presents upon its upper surface ridges much less strongly marked than those of the underlying true skin. This layer is rather thinner than the horny layer, is whitish in color, and is composed of a number of strata of elongated, prismoidal, nucleated cells, arranged perpendicularly to the matrix.

The horny layer, which constitutes the true nail, is applied by its under surface directly to the ridges of the Malpighian layer. It is dense and brittle and is composed of strata of flattened cells which can not be isolated without the use of reagents. If the different strata of this portion of the nail be studied after boiling in a dilute solution of sodium or potassium hydrate, it becomes evident that here, as in the horny layer of the epidermis, the lower cells are rounded, while those nearer the surface are flattened. These cells are nearly all nucleated. The thickness of this layer varies in different portions of the nail, while that of the Malpighian layer is nearly uniform. This layer is constantly growing, and it constitutes the entire substance of the free borders of the nails.

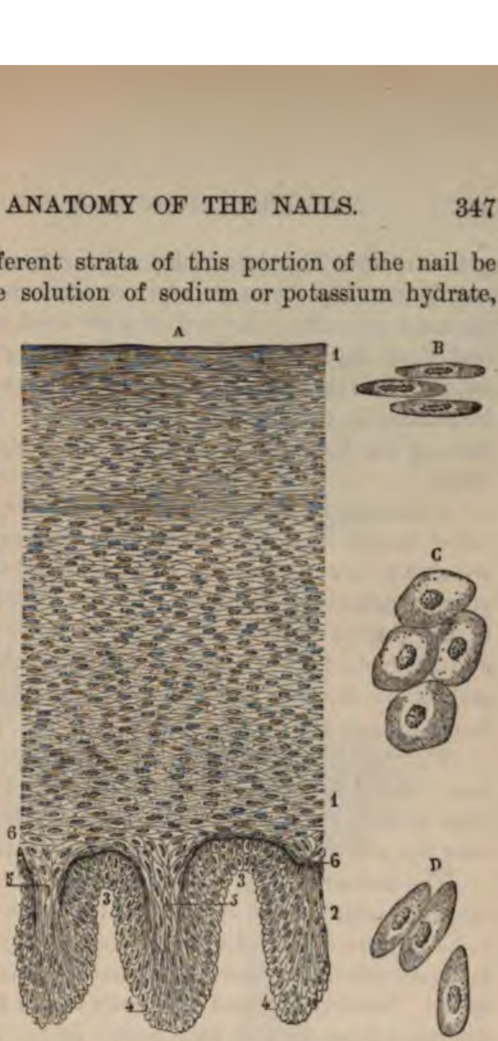


FIG. 106.—*Section of the nail etc.* (Sappey).
A, section of the nail: 1, 1, superficial layer; 2, deep layer; 3, 3, 4, 4, section of the grooves on the attached surface; 5, 5, union of the superficial with the deep layer; 6, 6, dark line between the two layers.
B, cells of the superficial layer, lateral view.
C, cells of the superficial layer, flat view.
D, cells of the deep layer.

The connections of the nails with the true skin resemble those of the epidermis; but the relations of these structures to the epidermis itself are somewhat peculiar. Before the fourth month of fœtal life, the epidermis covering the dorsal surfaces of the last phalanges of the fingers and toes does not present any marked peculiarities; but at about the fourth month, the peculiar hard cells of the horny layer of the nails make their appearance between the Malpighian and the horny layer of the epidermis, and at the same time the Malpighian layer beneath this plate, which is destined to become the Malpighian layer of the nails, is thickened and the cells assume a more elongated form. The horny layer of the nails constantly thickens from this time; but until the end of the fifth month, it is covered by the horny layer of the epidermis. After the fifth month, the epidermis breaks away and disappears from the surface; and at the seventh month, the nails begin to increase in length. Thus, at one time, the nails are actually included between the two layers of the epidermis; but after they have become developed, they are simply covered at their roots by a narrow border of the horny layer. The nails are therefore to be regarded as modifications of the horny layer of the epidermis, possessing certain anatomical and chemical peculiarities. The Malpighian layer of the nails is continuous with the same layer of the epidermis, but the horny layers are distinct.

One of the most striking peculiarities of the nails is their mode of growth. The Malpighian layer is stationary, but the horny layer is constantly growing, if the nails be cut, from the root and bed. It is evident that the nails grow from the bed, as their thickness progressively increases in the body from the root to near the free border; but their longitudinal growth is by far the more rapid. Indeed, the nails are constantly pushing forward, increasing in thickness as they advance. Near the end of the body of the nail, as the horny layer becomes thinner, the growth from below is diminished.

*Physiological Anatomy of the Hairs.*—Hairs, varying greatly in size, cover nearly every portion of the cutaneous surface. The only parts in which they are not found are the palms of the hands and soles of the feet, the palmar surfaces of the fingers and toes, the dorsal surfaces of the last phalanges of the fingers and toes, the lips, the upper eyelids, the lining of the prepuce and the glans penis. Some of the hairs are long, others are short and stiff, and others are fine and downy. These differences have led to a division of the hairs into three varieties:

The first variety includes the long, soft hairs, which are found on the head, on the face in the adult male, around the genital organs and under the arms in both the male and the female, and sometimes upon the breast and over the general surface of the body and extremities, particularly in the male.

The second variety, the short, stiff hairs, is found just within the nostrils, upon the edges of the eyelids and upon the eyebrows.

The third variety, the short, soft, downy hairs, is found on parts of the general surface not occupied by the long hairs, and in the caruncula lachrymalis. In early life, and ordinarily in the female at all ages, the trunk and extremities are covered with downy hairs; but in the adult male, these frequently become developed into long, soft hairs.

The hairs are usually set obliquely in the skin and take a definite direction as they lie upon the surface. Upon the head and face, and, indeed, the entire surface of the body, the general course of the hairs may be followed out, and they present currents or sweeps that have nearly always the same directions in different persons.

The diameter and length of the hairs are variable in different persons, especially in the long, soft hairs of the head and beard. It may be stated in general terms that the long hairs attain the length of twenty inches to three feet (500 to 900 mm.) in women, and considerably less in men. Like the nails, the hair, when left to itself, attains in three or four years a definite length, but when it is habitually cut it grows constantly. The short, stiff hairs are $\frac{1}{4}$ to $\frac{1}{2}$ of an inch (6·4 to 12·7 mm.) in length. The soft, downy hairs measure ordinarily $\frac{1}{12}$ to $\frac{1}{2}$ of an inch (2·1 to 12·7 mm.) in length.

Of the long hairs, the finest are upon the head, where they average about $\frac{1}{400}$ of an inch (64 $\mu$) in diameter. The hair ordinarily is coarser in women than in men. Dark hair is generally coarser than light hair; and upon the same head the extremes of variation are sometimes observed. The hairs of the beard and the long hairs of the body are coarser than the hairs of the head. The average number of hairs upon a square inch of the scalp is about 1,000 (155 in a square centimetre) and the number upon the entire head, about 120,000 (Wilson).

When the hairs are in a perfectly normal condition, they are very elastic and may be stretched to one-fifth or one-third more than their original

FIG. 107.—*Hair and hair-follicle* (Sappey).

1, root of the hair; 2, bulb of the hair; 3, internal root-sheath; 4, external root-sheath; 5, membrane of the hair-follicle (the internal, amorphous membrane of the follicle is very delicate and is not represented in the figure); 6, external membrane of the follicle; 7, 7, muscular bands attached to the follicle; 8, 8, extremities of these bands passing to the skin; 9, compound sebaceous gland, with its duct (10) opening into the upper third of the follicle; 11, simple sebaceous gland; 12, opening of the hair-follicle.

FIG. 108.—*Root of the hair* (Sappey).

1, root of the hair; 2, hair-bulb; 3, papilla of the follicle; 4, opening of the follicle; 5, 5, internal root-sheath; 6, external root-sheath; 7, 7, sebaceous glands; 8, 8, excretory ducts of the sebaceous glands.

length. Their strength varies with their thickness, but an ordinary hair from the head will bear a weight of six to seven ounces (170 to 200 grammes). A well known property of the hair is that of becoming strongly electric by friction; and this is particularly marked when the weather is cold and dry. The electricity thus excited is negative. Sections of the shaft of the hairs show that they are oval, but their shape is very variable, straight hairs being nearly round, while curled hairs are quite flat. Another peculiarity of the hairs is that they are strongly hygrometric. They readily absorb moisture and become sensibly elongated, a property which has been made use of by physicists in the construction of delicate hygrometers.

*Roots of the Hairs, and Hair-follicles.*—The roots of the hairs are embedded in follicular openings in the skin, which differ in the different varieties only in the depth to which they penetrate the cutaneous structure. In the downy hairs, the roots pass only into the superficial layers of the true skin; but in the thicker hairs, the roots pass through the skin and penetrate the subcutaneous cellulo-adipose tissue.

The root of the hair is softer, rounder and a little larger than the shaft. It becomes enlarged into a rounded bulb at the bottom of the follicle, and rests upon a fungiform papilla, constricted at its base, to which the hair is closely attached.

The hair-follicles are tubular inversions of the structures that compose the corium, and their walls present three membranes. Their length is $\frac{1}{12}$ to $\frac{1}{4}$ of an inch (2·1 to 6·4 mm.). The membrane that forms the external coat of the follicles is composed of inelastic fibres, generally arranged longitudinally. It is provided with blood-vessels, a few nerves and some connective-tissue elements, but no elastic tissue. This is the thickest of the three membranes and is closely connected with the corium. Next to this, is a fibrous membrane composed of fusiform, nucleated fibres arranged transversely. These resemble non-striated muscular fibres. The internal membrane is structureless and corresponds to the amorphous layer of the true skin. The papilla at the bottom of the hair-sac varies in size with the size of the hairs and is connected with the fibrous layers of the walls of the follicle. It is composed of amorphous matter, with a few granules and nuclei, and it probably contains blood-vessels and nerves, although these are not very distinct.

Although the different membranes of the hair-follicles are sufficiently recognizable, it is evident that the hair-sac is nothing more than an inversion of the corium, with certain modifications in the character and arrangement of its anatomical elements. The fibrous membranes correspond to the deeper layers of the true skin, without the elastic elements; and they present a peculiar arrangement of its inelastic fibres, the external fibres being longitudinal and the internal fibres transverse. The structureless membrane corresponds to the upper layers of the true skin, which are composed chiefly of amorphous matter. The hair-papilla corresponds to the papillæ on the general surface of the corium.

The investment of the root of the hair presents two distinct layers called the external and internal root-sheaths. The external root-sheath is three or four times as thick as the inner membrane, and it corresponds exactly with the Malpighian layer of the epidermis. This sheath is continuous with the bulb of the hair. The internal root-sheath is a transparent membrane, composed of flattened cells, generally without nuclei. This extends from the bottom of the hair-follicle and covers the lower two-thirds of the root.

*Structure of the Hairs.*—The different varieties of hairs present certain peculiarities in their anatomy, but all of them are composed of a fibrous structure forming the greater part of their substance, covered by a thin layer

FIG. 109.—*Human hair from the head of a white child; magnified 370 diameters* (from a photograph taken at the United States Army Medical Museum).

This figure shows the imbricated arrangement of the epidermis of the hair.

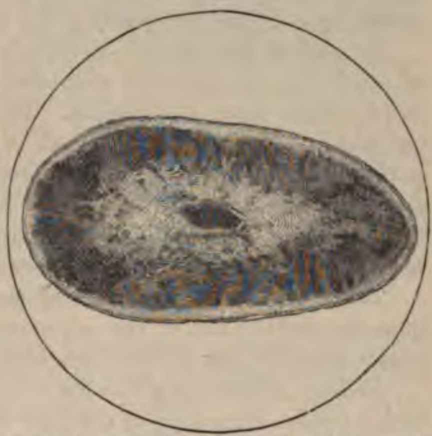

FIG. 110.—*Transverse section of a human hair from the beard of a white adult; magnified 370 diameters* (from a photograph taken at the United States Army Medical Museum).

of imbricated cells. In the short, stiff hairs, and in the long, white hairs, there is a distinct medullary substance; but this is wanting in the downy hairs and is indistinct in many of the long, dark hairs.

The fibrous substance of the hairs is composed of hard, elongated, longitudinal fibres, which can not be isolated without the aid of reagents. They may be separated, however, by maceration in warm sulphuric acid, when they present themselves in the form of dark, irregular, spindle-shaped plates. These contain pigmentary matter of various shades of color, occasional cavities filled with air, and a few nuclei. The pigment may be of any shade, between a light yellow and an intense black; and it is this substance that gives to the hair the great variety in color which is observed in different persons. In the lower part of the root the fibres are much shorter, and at the bulb they become transformed, as it were, into the soft, rounded cells found in this situation, covering the papilla.

The epidermis of the hair is very thin and is composed of flattened, quadrangular plates, overlying each other from below upward. These scales, or plates, are without nuclei, and they exist in a single layer over the shaft of the hair and the upper part of its root; but in the lower part of the root, the cells are thicker, softer, are frequently nucleated, and they exist in two layers.

The medulla is found in the short, stiff hairs, and it is often very distinct in the long, white hairs of the head. It occupies one-fourth to one-third of the diameter of the hair. The medulla can be traced, under favorable conditions, from just above the bulb to near the pointed extremity of the hair. It is composed of small, rounded, nucleated cells, which frequently contain dark granules of pigmentary matter. Mixed with these cells are air-globules; and frequently the cells are interrupted for a short distance and the space is filled with air. The medulla likewise contains a glutinous fluid between the cells and surrounding the air-globules.

*Growth of the Hairs.*—Although not provided with blood and devoid of sensibility, the hairs are connected with vascular parts and are nourished by imbibition from the papillæ. Each hair is first developed in a closed sac, and at about the sixth month of intraüterine life, its pointed extremity perforates the epidermis. These first-formed hairs are afterward shed, like the milk-teeth, being pushed out by new hairs from below, which latter arise from a second and a more deeply seated papilla. This shedding of the hairs usually takes place between the second and the eighth month after birth.

The difference in the color of the hair depends upon differences in the quantity and the tint of the pigmentary matter; and in old age the hair becomes white or gray from a blanching of the cortex and medulla.

*Sudden Blanching of the Hair.*—There are a few instances on record in which sudden blanching of the hair has been observed and the causes of this remarkable phenomenon fully investigated by competent observers; and it is almost unnecessary to say that a single, well authenticated case of this kind demonstrates the possibility of its occurrence and is important in connection with the reported instances which have not been subjected to proper investigation. One of these cases has been reported by Landois. In this instance the blanching of the hair occurred in a hospital in a single night, while the patient, who had an acute attack of delirium tremens, was under the daily observation of the visiting physician.

The microscopical examinations by Landois and others leave no doubt as to the cause of the white color of the hair in cases of sudden blanching; and the fact of the occurrence of this phenomenon can no longer be called in question. All are agreed that there is no diminution in the pigment, but that the greater part of the medulla becomes filled with air, small globules being also found in the cortical substance. The hair in these cases presents a marked contrast with hair that has gradually become gray from old age, when there is always a loss of pigment in the cortex and medulla. How the air finds its way into the hair in sudden blanching, it is difficult to understand; and the views that have been expressed on this subject by different authors are entirely theoretical.

The fact that the hair may become white or gray in the course of a few hours renders it probable that many of the cases reported upon unscientific authority actually occurred; and these have all been supposed to be connected with intense grief or terror. The terror was very marked in the case reported by Landois. In the great majority of recorded observations, the sudden blanching of the hair has been apparently connected with intense mental emotion; but this is all that can be said on the subject of causation, and the mechanism of the change is not understood.

*Uses of the Hair.*—The hairs serve an important purpose in the protection of the general surface and in guarding certain of the orifices of the body. The hair upon the head and the face protects from cold and shields the head from the rays of the sun during exposure in hot climates. Although the quantity of hair upon the general surface is small, as it is a very imperfect conductor of caloric, it serves in a degree to maintain the heat of the body. It also moderates the friction upon the surface. The eyebrows prevent the perspiration from running from the forehead upon the lids; the eyelashes protect the surface of the conjunctiva from dust and other foreign matters; the mustache protects the lungs from dust, which is very important in persons exposed to dust in long journeys or in their daily work; and the short, stiff hairs at the openings of the ears and nose protect these orifices. It is difficult to assign any special office to the hairs in some other situations, but their general uses are sufficiently evident.

## PERSPIRATION.

In the fullest acceptation of the term, perspiration embraces the entire action of the skin as an excreting organ and includes the exhalation of carbon dioxide as well as of watery vapor and organic matters. The office of the skin as an eliminator is undoubtedly very important; but the quantity of excrementitious matters with the properties of which physiologists are well acquainted, such as carbon dioxide and urea, thrown off from the general surface, is small as compared with what is exhaled by the lungs and discharged by the kidneys. If the surface of the body be covered with an impermeable coating, death occurs in a very short time; but the phenomena which precede the fatal result are difficult to explain. All that can be said upon this point is that death takes place when the heat of the body has been reduced to about 70° Fahr. (21° C.), and that suppression of the action of the skin in this way is always followed by a depression of the animal temperature. Warm-blooded animals die usually when more than one-half of the general surface has been varnished. Rabbits die when one-fourth of the surface has been covered with an impermeable coating (Laschkewitsch). Valentin and Laschkewitsch found that when the temperature was kept at about the normal standard by artificial means, no morbid symptoms were developed. The cause of death in these experiments has never been satisfactorily explained; and it is not easy to understand why coating the surface should be followed by such a rapid diminution in the general temperature. The experimental facts, however, indicate that the skin probably possesses important uses with which physiologists are unacquainted. Urea and some other effete products have been detected in the perspiration, but it is probable that some volatile matters are eliminated by the general surface, which have thus far escaped observation.

*Sudoriparous Glands.*—With few exceptions, every portion of the skin is provided with sudoriparous glands. They are not found, however, in the skin covering the concave surface of the concha of the ear, the glans penis, the inner lamella of the prepuce, and unless the ceruminous glands be regarded as sudoriparous organs, in the external auditory meatus.

On examining the surface of the skin with a low magnifying power, especially on the palms of the hands and the soles of the feet, the orifices of the sudoriferous ducts may be seen in the middle of the papillary ridges, forming a regular line in the shallow groove between the two rows of papillæ. The tubes always open upon the surface obliquely. In a thin section of the skin, the ducts are seen passing through the different layers and terminating in rounded, convoluted coils in the subcutaneous structure. These little, rounded or ovoid bodies, which are the sudoriparous, or sweat-producing structures, may be seen attached to the under surface of the skin when it has been removed from the subjacent parts by maceration. A perspiratory gland consists, indeed, of a simple tube, presenting a coiled mass, the sudoriparous portion, beneath the skin, and a tube of greater or less length, in proportion to the thickness of the cutaneous layers, which is the excretory duct, or the sudoriferous portion.

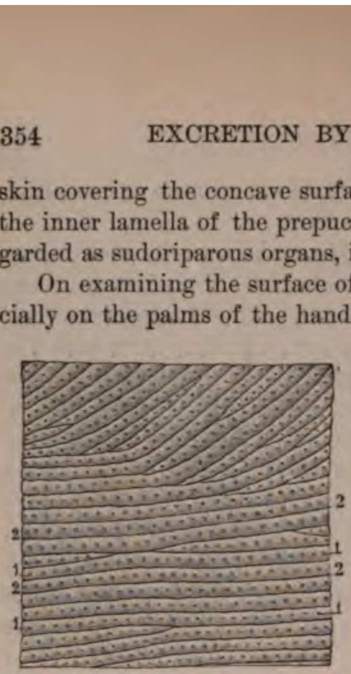


FIG. 111.—*Surface of the palm of the hand, a portion of the skin about one-half an inch (12·7 mm.) square; magnified 4 diameters* (Sappey).
1, 1, 1, 1, openings of the sudoriferous ducts; 2, 2, 2, 2, grooves between the papillæ of the skin.

The glandular coils are $\frac{1}{125}$ to $\frac{1}{25}$ of an inch (0·2 to 1 mm.) in diameter; the smallest coils being found beneath the skin of the penis, the scrotum, the eyelids, the nose and the convex surface of the concha of the ear, and the largest, on the areola of the nipple and the perineum. Very large glands are found mixed with smaller ones in the axilla, and these produce a peculiar secretion. The coiled portion of the tube is about $\frac{1}{310}$ of an inch (0·07 mm.) in diameter, and presents six to twelve turns. It consists of a sharply defined, strong, external membrane, which is very transparent, uniformly granular and sometimes indistinctly striated. The tube is of uniform diameter throughout the coil and terminates in a very slightly dilated, rounded, blind extremity. It is filled with epithelium in the form of finely granular matter, usually not segmented into cells, and is provided with small, oval nuclei. The glandular mass is surrounded by a plexus of capillary blood-vessels, which send a few small branches between the convolutions of the coil. Sometimes the coil is enclosed in a delicate fibrous envelope.

The excretory duct is simply a continuation of the glandular coil. Its course through the layers of the true skin is nearly straight. It then passes into the epidermis, between the papillæ of the corium, and presents, in this layer, a number of spiral turns. The spirals vary in number according to the thickness of the epidermis. Six to ten are found in the palms of the hands and twelve to fifteen in the soles of the feet (Sappey). As it emerges from the glandular coil, the excretory duct is somewhat narrower than the tube in the secreting portion; but as it passes through the epidermis, it again becomes larger. It possesses the same external membrane as the glandular coil and is lined generally by two layers of cells.

In a section of the skin and the subcutaneous tissue, involving several of the sudoriparous glands with their ducts, it is seen that the glandular coils generally are situated at different planes beneath the skin, as is indicated in Fig. 112.

FIG. 112.—*Sudoriparous glands; magnified 20 diameters* (Sappey).

1, 1, epidermis; 2, 2, mucous layer; 3, 3, papillæ; 4, 4, derma; 5, 5, subcutaneous areolar tissue; 6, 6, 6, 6, sudoriparous glands; 7, 7, adipose vesicles; 8, 8, excretory ducts in the derma; 9, 9, excretory ducts divided.

Sudoriparous glands in the axilla have been described which do not differ so much from the glands in other parts in their anatomy as in the character of their secretion. The coil in these glands is much larger than in other parts, measuring $\frac{1}{25}$ to $\frac{1}{12}$ of an inch (1 to 2 mm.); the walls of the tube are thicker, and they present an investment of fibrous tissue with an internal layer of longitudinal, non-striated muscular fibres; and finally, the tubes of the coil itself are lined with cells of epithelium. These glands are very abundant in the axilla, forming a continuous layer beneath the skin. Mixed with these, are a few glands of the ordinary variety.

Estimates have been made of the number of sudoriparous glands in the body and the probable extent of the exhalant surface of the skin, but they are to be taken as merely approximate. Krause found great differences in the number of perspiratory openings in different portions of the skin; but taking an average for the entire surface, it was estimated that the entire number of perspiratory glands is 2,381,248; and assuming that each coil when unravelled measures about $\frac{1}{16}$ of an inch (1·8 mm.), the entire length of the secreting tubes is about $2\frac{1}{3}$ miles ($3\frac{3}{4}$ kilometres). It must be remembered, however, that the length of the secreting coil only is given, and that the excretory ducts are not included.

*Mechanism of the Secretion of Sweat.*—The action of the skin as a glandular organ is continuous and not intermittent; but under ordinary conditions, the sweat is exhaled from the general surface in the form of vapor. With regard to the mechanism of its separation from the blood, nothing is to be said in addition to the general remarks upon the subject of secretion; and it is probable that the epithelium of the secreting coils is the active agent in the selection of the peculiar matters which enter into its composition. There are no examples of the separation by glandular organs of vapor from the blood, and the perspiration is secreted as a liquid, which becomes vaporous as it is discharged upon the surface.

The influence of the nervous system upon the secretion of sweat is important. It is well known, for example, that an abundant production of perspiration is frequently the result of mental emotions. Bernard has shown that the nervous influence may be exerted through the sympathetic system. He divided the sympathetic in the neck of a horse, producing as a consequence an elevation in temperature and an increase in the arterial pressure in the part supplied with branches of the nerve. He found, also, that the skin of the part became covered with a copious perspiration. Upon stimulating the divided extremity of the nerve, the secretion of sweat was arrested. The local secretion of sweat after division of the sympathetic in the neck of the horse was first observed by Dupuy, in 1816.

The stimulation as well as the division of certain nerves induces local secretion of sweat, but this is nearly always associated with dilatation of the blood-vessels of the part; still, sweat is frequently secreted when the surface is pale and bloodless, showing that dilatation of the blood-vessels is not an indispensable condition. The action of the so-called vaso-dilator nerves will be treated of in connection with the physiology of the nervous system. In experiments upon the cat, excito-secretory fibres have been found to exist in the cerebro-spinal nerves going to the anterior extremities. The fibres for the posterior extremities are in the sheath of the sciatic nerve. In all instances the action of these nerves is direct and not reflex. Experiments upon the cat have been very satisfactory, as this animal sweats only on the soles of the feet, and the secretion can be readily observed.

The so-called sweat-centres are in the lower part of the dorsal region of the spinal cord, for the posterior extremities, and in the lower part of the cervical region of the cord, for the anterior extremities. According to Adamkiewicz, both of these centres are subordinate to the principal sweat-centre, which is situated in the medulla oblongata. Ott has collected a number of cases of disease of the cord in the human subject, which go far to confirm the results of experiments on the inferior animals, with regard to the action of excito-secretory nerves and sweat-centres.

When the skin is in a normal condition, after exercise or whenever there is a tendency to elevation of the animal temperature, there is a determination of blood to the surface, accompanied with an increase in the secretion of sweat. This is the case when the body is exposed to a high temperature; and it is by an increase in the transpiration from the surface that the animal heat is maintained at the normal standard.

*Quantity of Cutaneous Exhalation.*—The quantity of cutaneous exhalation is subject to great variations, depending upon conditions of temperature and moisture, exercise, the quantity and character of the ingesta, etc. Most of these variations relate to the action of the skin in regulating the temperature of the body; and it is probable that the elimination of excrementitious matters by the skin is not subject, under normal conditions, to the same modifications, although positive experiments upon this point are wanting. When there is such a wide range of variation in different individuals and in the same person under different conditions of season, climate etc., it is possible only to give approximate estimates of the quantity of sweat secreted and exhaled in the twenty-four hours. Seguin and Lavoisier (1790) estimated the daily quantity of cutaneous transpiration at one pound and fourteen ounces (850 grammes), and the results of their observations have been fully confirmed by recent investigations. It may be assumed that the average quantity is nearly two pounds, or about 900 grammes.

Under violent and prolonged exercise, the loss of weight by exhalation from the skin and lungs may become very considerable. It is stated by Maclaren, the author of a work on training, that in one hour's energetic fencing, the loss by perspiration and respiration, taking the average of six consecutive days, was forty ounces (1,130 grammes), with a range of variation of eight ounces (227 grammes).

When the body is exposed to a high temperature, the exhalation from the surface is largely increased; and it is by this rapid evaporation that persons have been able to endure for several minutes a dry heat considerably exceeding that of boiling water. Southwood Smith made a series of observations with regard to this point upon workmen employed about the furnaces of gas-works and exposed to intense heat; and he found that in an hour, the loss of weight was two to four pounds (907 to 1,814 grammes), this being chiefly by exhalation of watery vapor from the skin. In such instances the loss of water by transpiration is compensated by the ingestion of large quantities of liquid.

*Properties and Composition of the Sweat.*—An analysis of the sweat was made by Favre, in 1853. After taking every precaution to obtain the secretion in a perfectly pure state, he collected a very large quantity, nearly thirty pints (14 litres), the result of six transpirations from one person, which he assumed to represent about the average in composition. The liquid was perfectly limpid, colorless, and of a feeble but characteristic odor. Almost all observers have found the reaction of the sweat to be acid; but it readily becomes alkaline on being subjected to evaporation, showing that it contains some of the volatile acids. Favre found that the fluid collected during the first half-hour of the observation was acid; during the second half-hour it was neutral or feebly alkaline; and during the third half-hour, it was constantly alkaline. The specific gravity of the sweat is 1003 to 1004. The following is the composition of the fluid collected by Favre:

COMPOSITION OF THE SWEAT.

| | | |
|---|---|---|
| Water | | 995·573 |
| Urea | | 0·043 |
| Fatty matters | | 0·014 |
| Alkaline lactates | | 0·317 |
| Alkaline sudorates | | 1·562 |
| Sodium chloride, | soluble in water | 2·230 |
| Potassium chloride, | soluble in water | 0·244 |
| Alkaline sulphates, | soluble in water | 0·012 |
| Alkaline phosphates, | soluble in water | a trace |
| Alkaline albuminates, | soluble in water | 0·005 |
| Alkaline earthy phosphates (soluble in acidulated water) | | a trace |
| Epidermic *débris* (insoluble) | | a trace |
| | | 1,000·000 |

The sweat is exhaled usually in the form of vapor, when it is known as insensible perspiration. When from any cause it collects on the surface, in the form of a liquid, it is called sensible perspiration.

The peculiar constituents of the sweat have been more carefully and successfully studied since the analyses of Favre. The neutral fats are probably derived in great part from the sebaceous glands, although certain fats, palmitine and stearine, have been found in the secretion of the palms of the hands, which contain no sebaceous glands. The volatile fatty acids are formic, butyric, caproic, capric, acetic etc., some of which exist also in milk. These give to the sweat its peculiar odor. Urea is always present in small quantity, and its proportion may be largely increased when there is a deficiency of elimination by the kidneys. It is a matter, also, of common as well as of scientific observation that the sweat is more abundant when the kidneys are comparatively inactive, and *vice versâ*. Generally, however, conditions operate to increase the quantity of sweat, and the quantity of urine is proportionally diminished. The skin is undoubtedly an important organ of excretion, and it may eliminate excrementitious matters of a character as yet unknown. The action of the skin as a respiratory organ has already been considered. With regard to the inorganic constituents of the sweat, there is no great interest attached to any but the sodium chloride, which exists in a proportion many times greater than that of all the other inorganic salts combined.

*Peculiarities of the Sweat in Certain Parts.*—In the axilla, the inguino-scrotal region in the male, and the inguino-vulvar region in the female, and between the toes, the sweat always has a peculiar odor, more or less marked, which in some persons is excessively disagreeable. Donné has shown that whenever the secretion has an odor of this kind its reaction is distinctly alkaline; and he is disposed to regard its peculiar characters as due to a mixture of the secretion of the other follicles found in these situations. Sometimes the sweat about the nose has an alkaline reaction. In the axillary region the secretion is rather less fluid than on the general surface and frequently has a yellowish color, so marked, sometimes, as to stain the clothing.

## Physiological Anatomy of the Kidneys.

The kidneys are symmetrical organs, situated in the lumbar region, beneath the peritoneum, invested by a proper fibrous coat, and always surrounded by more or less adipose tissue. They usually extend from the eleventh or twelfth rib downward to near the crest of the ilium, and the right is always a little lower than the left. In shape the kidney is very appropriately compared to a bean; and the concavity, the deep, central portion of which is called the hilum, looks inward toward the spinal column. The weight of each kidney is four to six ounces (113 to 170 grammes), usually about half an ounce (14 grammes) less in the female than in the male. The left kidney is nearly always a little heavier than the right.

Outside of the proper coat of the kidney, is a certain quantity of adipose tissue enclosed in a loose, fibrous structure. This is sometimes called the adipose capsule; but the proper coat consists of a close net-work of ordinary fibrous tissue, interlaced with small elastic fibres. This coat is thin and smooth and may be readily removed from the surface of the organ, At the hilum it is continued inward to line the pelvis of the kidney, covering the calices and blood-vessels.

The kidney in a vertical section presents a cavity at the hilum, which is bounded internally by the dilated origin of the ureter. This is called the pelvis. It is lined by a smooth membrane, which is simply a continuation of the proper coat of the kidney, and which forms little cylinders, called calices, into which the apices of the pyramids are received. Some of the calices receive the apex of a single pyramid, while others are larger and receive two or three. The calices unite into three short, funnel-shaped tubes, called infundibula, corresponding respectively to the superior, middle and inferior portions of the kidney. These finally open into the common cavity, or pelvis. The substance of the kidney is composed of two distinctly marked portions, called the cortical substance, and the medullary, or pyramidal substance.

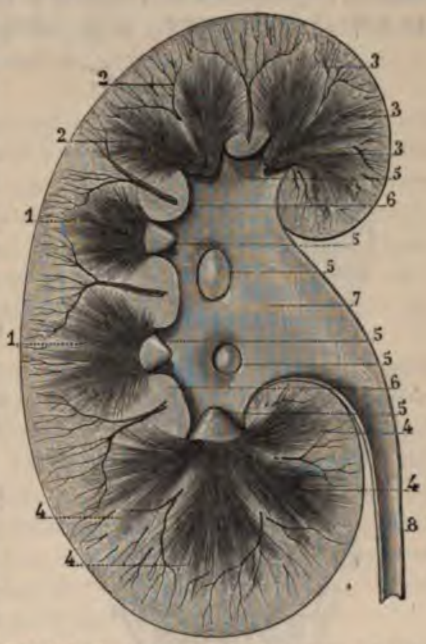

FIG. 113.—*Vertical section of the kidney* (Sappey). 1, 1, 2, 2, 3, 3, 3, 4, 4, 4, 4, pyramids of Malpighi; 5, 5, 5, 5, 5, 5, apices of the pyramids, surrounded by the calices; 6, 6, columns of Bertin; 7, pelvis of the kidney; 8, upper extremity of the ureter.

The cortical substance is reddish and granular, rather softer than the pyramidal substance, and is about one-sixth of an inch (4·2 mm.) in thickness. This occupies the exterior of the kidney and sends little prolongations, called the columns of Bertin, between the pyramids. The surface of the kidney is marked by little, polygonal divisions, giving it a lobulated appearance. This, however, is mainly due to the arrangement of the superficial blood-vessels. The medullary substance is arranged in the form of pyramids, sometimes called the pyramids of Malpighi, twelve, fifteen or eighteen in number, their bases presenting toward the cortical substance, and their apices being received into the calices, at the pelvis. Ferrein subdivided the pyramids of Malpighi into smaller pyramids, called the pyramids of Ferrein, each formed by about one hundred tubes radiating from the openings at the summit of the pyramids, toward their bases. The tubes composing these pyramids pass into the cortical substance, forming corresponding pyramids of convoluted tubes, thus dividing this portion of the kidney into lobules, more or less distinct.

The medullary substance is firm, of a darker red color than the cortical substance, and is marked by tolerably distinct striæ, which take a nearly straight course from the bases to the apices of the pyramids. As these striæ indicate the direction of the little tubes that constitute the greatest part of the medullary substance, this is sometimes called the tubular portion of the kidney.

From the arrangement of the secreting portion of the kidneys, these organs are classed among the tubular glands, presenting a system of tubes, or canals, some of which are supposed simply to carry off the urine, while others separate the excrementitious constituents of this fluid from the blood. It is difficult to determine precisely where the secreting tubes merge into the excretory ducts, but it is the common idea, which is probably correct, that the cortical substance is the active portion, while the tubes of the pyramidal portion simply carry off the excretion.

*Pyramidal Substance.*—Each papilla, as it projects into the pelvis of the kidney, presents ten to twenty-five little openings, $\frac{1}{300}$ to $\frac{1}{60}$ of an inch (85 to 425 $\mu$) in diameter. The tubes leading from the pelvis immediately

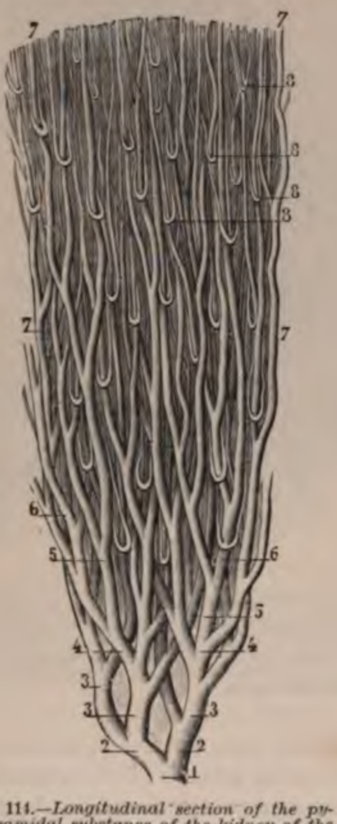

FIG. 114.—*Longitudinal section of the pyramidal substance of the kidney of the fœtus* (Sappey).

1, trunk of a large uriniferous tube; 2, 2, primary branches of this tube; 3, 3, 3, secondary branches; 4, 4, 5, 5, 6, 6, 7, 7, 7, 7, branches becoming smaller and smaller; 8, 8, 8, 8, loops of the tubes of Henle.

FIG. 115.—*Longitudinal section of the cortical substance of the same kidney* (Sappey).

1, 1, limit of the cortical substance and base of the pyramids; 2, 2, 2, tubes passing toward the surface of the kidney; 3, 3, 3, 8, 8, 8, convoluted tubes; 4, 4, 4, 4, 5, Malpighian bodies; 6, 6, artery, with its branches (7, 7, 7); 9, 9, fibrous covering of the kidney.

divide at very acute angles, generally dichotomously, until a bundle of tubes arises, as it were, from each opening. These bundles constitute the pyramids of Ferrein. In their course the tubes are slightly wavy and are nearly parallel to each other. These are called the straight tubes of the kidney, or the tubes of Bellini. They extend from the apices of the pyramids to their bases and pass then into the cortical substance. The pyramids contain, in addition to the straight tubes, a delicate, fibrous matrix and blood-vessels, which latter generally pass beyond the pyramids, to be finally distributed in the cortical substance. Small tubes, continuous with the convoluted tubes of the cortical substance, dip down into the pyramids, returning to the cortical substance in the form of loops. This arrangement will be fully described in connection with the cortical substance.

The tubes of the pyramidal substance are composed of a strong, structureless basement-membrane, lined with granular, nucleated cells. According to Bowman, the tubes measure $\frac{1}{300}$ to $\frac{1}{200}$ of an inch (85 to 127 $\mu$), in diameter at the apices, and near the bases of the pyramids their diameter is about $\frac{1}{600}$ of an inch (42 $\mu$).

The cells lining the straight tubes exist in a single layer applied to the basement-membrane. They are thick and irregularly polygonal in shape, with abundant albuminoid granules. They present one, and occasionally, though rarely, two granular nuclei, with one or two nucleoli. They readily undergo alteration and are seen in their normal condition only in a perfectly fresh, healthy kidney. Their diameter is about $\frac{1}{1500}$ of an inch (17 $\mu$). The caliber of the tubes is reduced by the thickness of their lining epithelium to $\frac{1}{900}$ or $\frac{1}{850}$ of an inch (28 or 30 $\mu$).

*Cortical Substance.*—In the cortical portion of the kidney, are found tubes, differing somewhat from the tubes of the pyramidal portion in their size and in the character of their epithelial lining, but presenting the most marked difference in their direction. These tubes are rather larger than the tubes of the pyramidal substance, and are very much convoluted, interlacing with each other in every direction. Scattered pretty uniformly throughout this portion of the kidney, are rounded or ovoid bodies, about four times the diameter of the convoluted tubes, known as the Malphigian bodies. These are simply flask-like, terminal dilatations of the tubes themselves.

The cortical portion of the kidney presents a delicate, fibrous matrix, which forms a support for the secreting portion and its blood-vessels. The tubes of the cortical substance present considerable variations in size, and three well defined varieties can be distinguished:

1. The ordinary convoluted tubes, directly connected with the Malpighian bodies. 2. Small tubes, continuous with the convoluted tubes, dipping down into the pyramids and returning to the cortical portion in the form of loops. 3. Communicating tubes, forming a plexus connecting the different varieties of tubes with each other and finally with the straight tubes of the pyramidal portion.

In tracing out the course of the tubes, it will be found most convenient to begin with a description of the Malpighian bodies and to follow the tubes from these bodies to their connections with the straight tubes of the pyramidal substance.

*Malpighian Bodies.*—These are ovoid or rounded, terminal dilatations of the convoluted tubes, and are $\frac{1}{250}$ to $\frac{1}{100}$ of an inch (100 to 250 $\mu$), in diameter. They are composed of a membrane, which is continuous with the external membrane of the convoluted tubes, and is of the same homogeneous character, but somewhat thicker. This sac, called the capsule of Müller or of Bowman, encloses a mass of convoluted blood-vessels and is lined with a layer of nucleated epithelial cells. In addition to the cells lining the capsule, there are other cells which are applied to the blood-vessels.

The cells attached to the capsule of Müller are smaller and more transparent than those lining the convoluted tubes. They are ovoid, nucleated and finely granular. The cells covering the vessels, however, are larger and more opaque, and they resemble the epithelium lining the tubes. They measure $\frac{1}{1400}$ to $\frac{1}{1000}$ of an inch (16 to 25 $\mu$), in diameter, by about $\frac{1}{2500}$ of an inch (10 $\mu$) in thickness.

*Tubes of the Cortical Substance.*—Passing from the Malpighian bodies, the tubes present first a short, constricted portion, called the neck of the capsule, which soon dilates to the diameter of about $\frac{1}{500}$ of an inch (50 $\mu$), when their course becomes quite intricate and convoluted. These are what are known as the convoluted tubes of the kidney. The membrane of these tubes is transparent and homogeneous, but quite firm and resisting. It is lined throughout with a single layer of epithelial cells, $\frac{1}{1400}$ to $\frac{1}{1000}$ of an inch (16 to 25 $\mu$) in diameter, somewhat larger, consequently, than the cells lining the straight tubes. The cells lining the convoluted tubes present two tolerably distinct portions. The inner portion or zone, which is next the lumen of the tube, is finely granular, with sometimes a few small oil-globules. The outer zone presents little fibrils or rods, which are perpendicular to the tubular membrane. These are called "rodded" cells, and a similar appearance is presented by some of the cells of the pancreas and of the salivary glands. The nucleus is usually situated between the granular and the rodded zones.

The researches of Heidenhain and others have shown that the greatest part of the solid excrementitious constituents of the urine, such as urea and the urates, is separated from the blood by the cells of the convoluted tubes of the cortical substance and perhaps by the dilated portions of the tubes of Henle, while the water and a certain portion of the inorganic salts of the urine transude through the blood-vessels in the Malpighian bodies. This view was first advanced by Bowman, in 1842.

*Narrow Tubes of Henle.*—The convoluted tubes above described, after a tortuous course in the cortical substance, become continuous, near the pyramids, with the tubes of much smaller diameter, which form loops extending to a greater or less depth into the pyramids. The loops formed by these canals (the narrow tubes of Henle), are nearly parallel with the tubes of Bellini and are much greater in number near the bases of the pyramids than toward the apices. The diameter of these tubes is very variable, and they present enlargements at irregular intervals in their course. The narrow portions are about $\frac{1}{2000}$ of an inch (12 $\mu$) in diameter, and the wide portions,

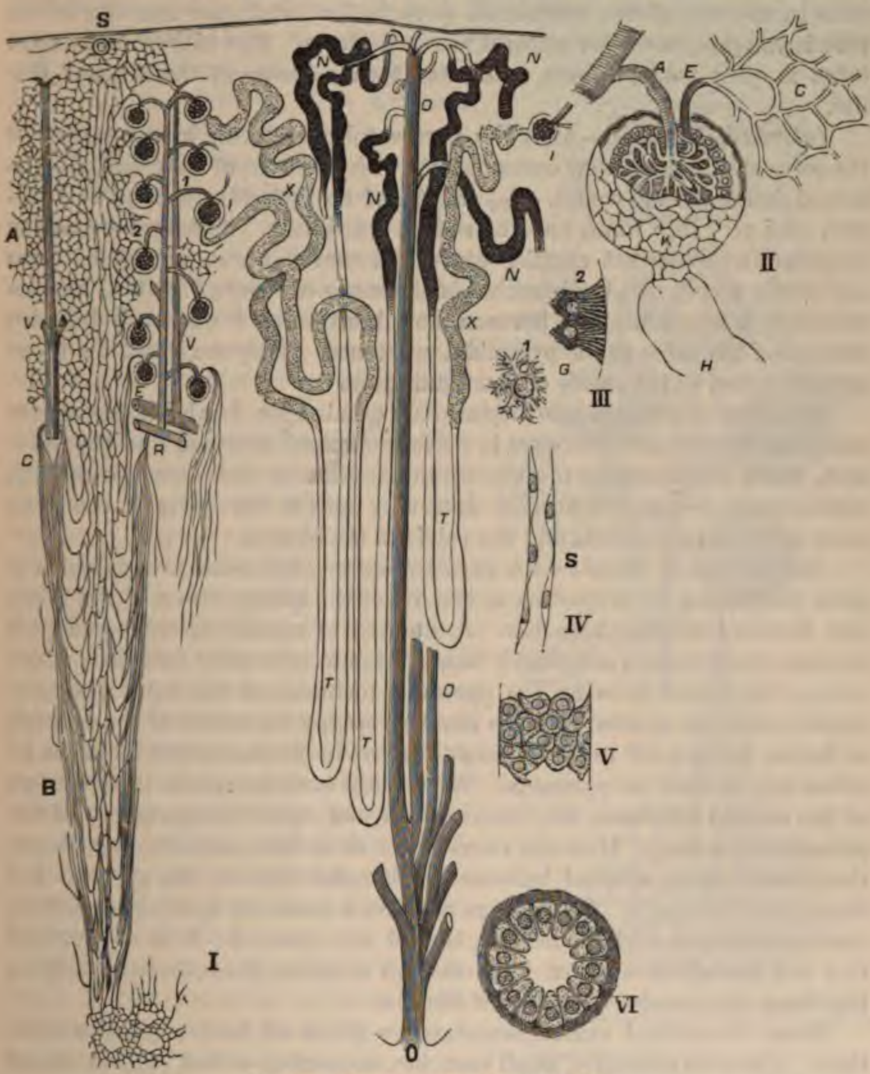


FIG. 116.—*Structure of the kidney* (Landois).

I, blood-vessels and tubes (semi-diagrammatic). A, capillaries of the cortical substance; B, capillaries of the medullary substance; 1, artery penetrating a Malpighian body; 2, vein emerging from a Malpighian body; R, arteriolæ rectæ; C, venæ rectæ; V, V, interlobular veins; S, stellate veins; I, I, capsules of Müller; X, X, convoluted tubes; T, T, T. tubes of Henle; N, N, N, N, communicating tubes; O, O, straight tubes; O, opening into the pelvis of the kidney.
II, Malpighian body. A, artery; E, vein; C, capillaries; K, epithelium of the capsule; H, beginning of a convoluted tube.
III, rodded cells from a convoluted tube. 1, view from the surface; 2, side view (G, granular zone).
IV, cells lining the tubes of Henle.
V, cells lining the communicating tubes.
VI, section of a straight tube.

about twice this size. The narrow portion is lined by small, clear cells with very prominent nuclei. The wider portions are lined by larger, granular cells. Near the bases of the pyramids the wide portion sometimes forms the loop, but near the apices the loop is always narrow. The difference in the size of the epithelium is such, that while the diameter of the tube is variable, its caliber remains nearly uniform. The membrane of these tubes is quite thick, thicker, even, than the membrane of the tubes of Bellini.

*Intermediate Tubes.*—After the narrow tubes of Henle have returned to the cortical substance, they communicate with a system of flattened, ribbon-shaped, anastomosing canals, $\frac{1}{1200}$ to $\frac{1}{1000}$ of an inch (21 to 25 $\mu$) in diameter, with very thin walls, lined by rodded epithelium. These tubes take an irregular and somewhat angular course between the true convoluted tubes and finally èmpty into the branches of the straight tubes of Bellini, thus establishing a communication between the tubes coming from the Malpighian bodies and the tubes of the pyramidal substance. They are called the intermediate tubes, or the canals of communication.

The tubes into which the intermediate canals open join with others generally two by two, and then pass in a nearly straight direction into the pyramids, where they continue to unite with each other in their course, becoming, consequently, reduced in number until they open at the apices of the pyramids, into the infundibula and the pelvis of the kidney.

*Distribution of Blood-vessels in the Kidney.*—The renal artery, which is quite voluminous in proportion to the size of the kidney, enters at the hilum and divides into four branches. A number of smaller branches penetrate between the pyramids and ramify in the columns of cortical substance which occupy the spaces between the pyramids (columns of Bertin). The main vessels, which are generally two in number, occupy the centre of the columns of Bertin, sending off in their course, at short intervals, regular branches on either side, toward the pyramids. When these branches reach the boundary of the cortical substance, they turn upward and follow the periphery of the pyramid to its base. Here the vessels form an arched, anastomosing plexus, the arterial arcade, situated between the rounded base of the pyramid and the cortical substance. This plexus presents a convexity looking toward the cortical substance, and a concavity, toward the pyramid. It is so arranged that the interstices are just large enough to admit the collections of tubes that form the so-called pyramids of Ferrein.

From the arterial arcade, branches are given off in two opposite directions. From its concavity, small branches, measuring at first $\frac{1}{1200}$ to $\frac{1}{750}$ of an inch (21 to 34 $\mu$) in diameter, pass downward toward the papillæ, giving off small ramifications at very acute angles, and becoming reduced in size to about $\frac{1}{2500}$ of an inch (10 $\mu$). These vessels, called sometimes the arteriolæ rectæ, surround the straight tubes, and pass into capillaries in the substance of the pyramids and at their apices.

From the convex surface of the arterial arcade, branches are given off at nearly right angles. These pass into the cortical substance, breaking up into a large number of little arterial twigs, $\frac{1}{1500}$ to $\frac{1}{600}$ of an inch (17 to 40 $\mu$) in diameter, each one of which penetrates a Malpighian body at a point opposite the neck of the capsule. Once within the capsule, the arteriole breaks up into five to eight branches, which then divide dichotomously into vessels measuring $\frac{1}{3000}$ to $\frac{1}{1500}$ of an inch (8 to 17 $\mu$) in diameter, arranged in the form of coils and loops, constituting a dense, rounded mass (the Malpighian coil, or glomerulus), filling the capsule. These vessels break up into capillaries without anastomoses.

The blood is collected from the vessels of the Malpighian bodies by veins, sometimes one and frequently three or four, which pass out of the capsule and form a second capillary plexus surrounding the convoluted tubes. When there is but one vein, it generally emerges from the capsule near the point of penetration of the arteriole.

The efferent vessels, immediately after their emergence from the capsule, break up into a very fine and delicate plexus of capillaries, closely surrounding the convoluted tubes. These form a true plexus, the branches anastomosing freely in every direction; and the distribution of vessels in this part resembles essentially the vascular arrangement in most of the glands. Bowman has called the branches which connect together the vessels of the Malpighian tuft and the capillary plexus surrounding the tubes, the portal system of the kidney. These intermediate vessels form a coarse plexus surrounding the prolongations of the pyramids of Ferrein into the cortical substance.

FIG. 117. — *Blood-vessels of the Malpighian bodies and convoluted tubes of the kidney* (Sappey).

1, 1, Malpighian bodies surrounded by the capsules of Müller; 2, 2, 2, convoluted tubes connected with the Malpighian bodies; 3, artery branching to go to the Malpighian bodies; 4, 4, 4, branches of the artery; 6, 6, Malpighian bodies from which a portion of the capsules has been removed; 7, 7, 7, vessels passing out of the Malpighian bodies; 8, vessel, the branches of which (9) pass to the capillary plexus (10).

The renal, or emulgent vein takes its origin in part from the capillary plexus surrounding the convoluted tubes and in part from the vessels distributed in the pyramidal substance. A few branches come from vessels in the envelopes of the kidney, but these are comparatively unimportant. The plexus surrounding the convoluted tubes empties into venous radicles which pass to the surface of the kidney, and these present a number of little radiating groups, each converging toward a central vessel. This arrangement gives to the vessels of the fibrous envelope of the kidney a peculiar, stellate appearance, forming what are sometimes called the stars of Verheyn. The large trunks which form the centres of these stars then pass through the cortical substance to the rounded bases of the pyramids, where they form a vaulted, venous plexus corresponding to the arterial plexus already described. The vessels distributed upon the straight tubes of the pyramidal substance form a loose plexus around these tubes, except at the papillæ, where the network is much closer. They then pass into the plexus at the bases of the pyramids to join with the veins from the cortical substance. From this plexus a number of larger trunks arise and pass toward the hilum, in the axis of the inter-pyramidal substance, enveloped in the same sheath with the arteries. Passing thus to the pelvis of the kidney, the veins converge into three or four great branches, which unite to form the renal, or emulgent vein. A preparation of all the vessels of the kidneys shows that the veins are much more voluminous than the arteries.

The capsule of the kidney has a lymphatic plexus connected with lymph-spaces below; and lymph-spaces, in the form of large slits, exist between and around the convoluted tubes.

The nerves are quite abundant and are derived from the solar plexus, their filaments following the renal artery in its distribution in the interior of the organ, and ramifying upon the walls of the vessels.

### Mechanism of the Production and Discharge of Urine.

The most important constituent of the urine is urea—$CO(NH_2)_2$—, a crystallizable, nitrogenized substance, which is discharged by the skin as well as by the kidneys. This has long been recognized as an excrementitious substance; but the first observations that gave any definite idea of the mechanism of its production were made by Prévost and Dumas, in 1821. At the time these experiments were made, chemists were not able to detect urea in the normal blood; but Prévost and Dumas extirpated the kidneys from living animals, dogs and cats, and found an abundance of urea in the blood, after certain symptoms of blood-poisoning had been developed. For the first two or three days after the operation there were no symptoms of blood-poisoning; but finally stupor and other marked evidences of nervous disturbance supervened, when the presence of urea in the blood could be easily determined. These observations were confirmed and extended by Ségalas and Vauquelin, in 1822. Since that time, as the processes for the determination of urea in the animal fluids have been improved, this substance has been detected in minute quantity in the normal blood. Picard (1856) estimated and compared the proportions of urea in the renal artery and the renal vein, and he found that the quantity in the blood was diminished by about one-half in its passage through the kidneys. Still later, urea has been found in the lymph and chyle, in larger quantity, even, than in the blood (Wurtz).

Bernard and Barreswil (1847) found that animals from which both kidneys had been removed did not usually present any distinctive symptoms for a day or two after, except that they vomited and passed an unusual quantity of liquid from the intestinal canal. During this time the blood never contained an abnormal quantity of urea; but the contents of the stomach and intestine were found to be highly ammoniacal, and the secretions from these parts, particularly the stomach, became continuous as well as increased in quantity. Animals operated upon in this way usually live for four or five days, and they then die in coma following convulsions. Toward the end of life, the secretion of gastric and intestinal fluids becomes arrested, probably from the irritating effects of ammoniacal decomposition of their contents, and then, and then only, urea is found to accumulate in the blood.

The results obtained by other experimenters have generally corresponded with those of Bernard and Barreswil. It has also been ascertained, as was shown by Ségalas and Vauquelin, that urea is an active diuretic when injected in small quantity into the veins of a healthy animal; and that in this case, it does not produce any poisonous effects, but is immediately eliminated. When urea is injected into the vascular system of a nephrotomized animal, it produces death in a very short time, with the characteristic symptoms of uræmic poisoning.

Experiments which were supposed to show that urea and the urates are formed in the kidneys have been made with the view of comparing the effects of removal of both kidneys with those produced by tying the ureters. According to these observations, the blood contains much more urea after the ureters are tied than after removal of the kidneys. These experiments, which are directly opposed in their results to the observations of Prévost and Dumas, Bernard and Barreswil, Ségalas, and many others, can not be accepted unless it be certain that all the necessary physiological conditions were fulfilled. In the first place, it was demonstrated, as early as 1847, that urea does not accumulate in the blood immediately after removal of the kidneys, but that this occurs only toward the end of life, and then urea is found in large quantity. In the second place, it is well known that the operation of tying the ureters is followed by a greatly increased pressure of urine in the kidneys, which not only disturbs the eliminative action of these organs but affects most seriously the general functions. Since the influence of the nervous system upon the secretions has been closely studied, it is evident that the pain and disturbance consequent upon the accumulation of urine above the ligated ureters must have an important reflex action upon the secretions; and this would probably interfere with the vicarious elimination of urea and of other excrementitious substances by the stomach and intestines. It is well known that an arrest of these secretions, in cases of organic disease of the kidneys, is liable to be followed immediately by evidences of uræmia, and that grave uræmic symptoms are frequently relieved by the administration of remedies that act promptly and powerfully upon the intestinal canal.

From a careful review of the important facts bearing upon the question under consideration, there does not seem to be any valid ground for a change in the ideas of physiologists concerning the mode of elimination of urea and the other important excrementitious constituents of the urine. There is every reason to suppose that these substances are produced in various tissues and organs of the body during the process of disassimilation, are taken up by the blood and are simply separated from the blood by the kidneys.

Extirpation of one kidney from a living animal is not necessarily fatal. If the operation be carefully performed, the wound will generally heal without difficulty, and in most instances the remaining kidney seems sufficient for the elimination of urine for an indefinite period. In a large number of experiments, the animals killed long after the wound had healed never presented any marked symptoms of retention of excrementitious matters in the blood, except in one or two instances. It is a noticeable fact, however, that in many instances they showed a marked change in disposition, and the appetite became voracious and unnatural. These animals would sometimes eat fæces, the flesh of dogs, etc., and, in short, presented certain of the phenomena so frequently observed after extirpation of the spleen (Flint). After extirpation of one kidney, it has been observed that the remaining kidney increases in weight, although investigations have shown that this is due mainly to an increase in the quantity of blood, lymph and urinary matters, and not to a new development of renal tissue. The following is an exceptional experiment in which the animal died after extirpation of one kidney: One kidney was removed from a small cur-dog, about nine months old, by an incision in the lumbar region. The animal did not appear to suffer from the operation, and the wound healed kindly. The only marked effects were great irritability of disposition and an exaggerated and perverted appetite. He would attack the other dogs in the laboratory without provocation, and would eat with avidity, fæces, putrid dog's flesh and articles which the other animals would not touch and which he did not eat before the operation. Forty-three days after the operation, the dog appeared to be uneasy, cried frequently, and went into convulsions, which continued for about three hours, when he died (Flint, 1864). In one other instance, in which a dog was kept for more than a year after extirpation of one kidney, it was occasionally observed that the animal was rather quiet and indisposed to move for a day or two, but this always passed off, and when he was killed he was as well as before the operation.

*Influence of Blood-pressure, the Nervous System etc., upon the Secretion of Urine.*—There are many instances in which very marked and sudden modifications in the action of the kidneys take place under the influence of fear, anxiety, hysteria etc., which must operate through the nervous system. Although little is known of the final distribution of the nerves in the kidney, it has been ascertained that here, as elsewhere, vaso-motor nerves are distributed to the walls of the blood-vessels, and they are capable of modifying the quantity and the pressure of blood in these organs.

It may be stated as a general proposition, that an increase in the pressure of blood in the kidneys increases the flow of urine, and that when the blood-pressure is lowered, the flow of urine is correspondingly diminished. This will in a measure account for the increase in the flow of urine during digestion; but it can not serve to explain all of the modifications that may take place in the action of the kidneys. Bernard measured the pressure of blood in the carotid artery of a dog and noted the quantity of urine discharged in the course of a minute from one of the ureters. Afterward, by tying the two crural, the two brachial and the two carotid arteries, he increased the blood-pressure about one-half, and the quantity of urine discharged in a minute was immediately increased by a little more than fifty per cent. In another animal, he diminished the pressure by taking blood from the jugular vein, and the quantity of urine was immediately reduced about one-half. He also showed that the increase in the quantity of urine produced by exaggerated pressure of blood in the kidneys could be modified through the nervous system. The nerves going to one kidney were divided, which produced an increase in the arterial pressure and a consequent exaggeration in the quantity of urine from the ureter on that side. The pressure was then farther increased by stopping the nostrils of the animal. The quantity of urine was increased by this on the side on which the nerves had been divided, but the pain and distress from want of air arrested the secretion upon the sound side.

When irritation is applied to the floor of the fourth ventricle, in the median line, exactly in the middle of the space between the origin of the pneumogastrics and the auditory nerves, the urine is increased in quantity and becomes strongly saccharine. When the irritation is applied a little above this point, the urine is simply increased in quantity, but it contains no sugar; and when a puncture is made a little below, sugar appears in the urine, without any increase in the quantity of the secretion (Bernard). It has also been observed that section of the spinal cord in the upper part of the dorsal region arrests, for a time, the secretion of urine.

Other physiological conditions that affect the urinary excretion influence the composition of the urine and the quantity of excrementitious matters separated by the kidneys. These will be fully considered in another place. It is sufficient to remark, in this connection, that during digestion, when the composition of the blood is modified by the absorption of nutritive matters, the quantity of urine usually is increased. This is particularly marked when a large quantity of liquid has been taken.

Inasmuch as the excrementitious matters eliminated by the kidneys are being constantly produced in the tissues by the process of disassimilation, the formation of urine is constant, presenting, in this regard, a marked contrast with the intermittent flow of most of the secretions proper as distinguished from the excretions. It was noted by Erichsen, in a case of extroversion of the bladder, and it has been farther shown by experiments upon dogs, that there is an alternation in the action of the kidneys upon the two sides. Bernard exposed the ureters in a living animal and fixed a small, silver tube in each, so that the secretion from either kidney could be readily observed; and he noted that a large quantity of fluid was discharged from one side for fifteen to thirty minutes, while the flow from the other side was slight and in some instances was arrested. The flow then began with activity upon the other side, while the discharge from the opposite ureter was diminished or arrested.

*Physiological Anatomy of the Urinary Passages.*—The excretory ducts of the kidneys, the ureters, begin each by a funnel-shaped portion, which is applied to the kidney at the hilum. The ureters themselves are membranous tubes of about the diameter of a goose-quill, becoming much reduced in caliber as they penetrate the coats of the bladder. They are sixteen to eighteen inches (40 to 46 centimetres) in length, and pass from the kidneys to the bladder, behind the peritoneum. They have three distinct coats: an external coat, composed of ordinary fibrous tissue, with small elastic fibres; a middle coat, composed of non-striated muscular fibres; and a mucous coat.

The external coat requires no special description. It is prolonged into the calices and is continuous with the fibrous coat of the kidney.

The fibres of the muscular coat, in the greatest part of the length of the ureters, interlace with each other in every direction and are not arranged in distinct layers; but near the bladder, is an internal layer, in which the direction of the fibres is longitudinal.

The mucous lining is thin, smooth and without any follicular glands. It is thrown into narrow, longitudinal folds, when the tube is flaccid, which are easily effaced by distention. The epithelium exists in several layers and is remarkable for the irregular shape of the cells. These present, usually, dark granulations and one or two clear nuclei with distinct nucleoli. Some of the cells are flattened, some are rounded, and some are caudate with one or two prolongations.

Passing to the base of the bladder, the ureters become constricted, penetrate the coats of this organ obliquely, their course in its walls being a little less than an inch (25 mm.) in length. This valvular opening allows the free passage of the urine from the ureters, but compression or distention of the bladder closes the orifices and renders a return of the fluid impossible.

The bladder, which serves as a reservoir for the urine, varies in its relations to the pelvic and abdominal organs as it is empty or more or less distended. When empty, it lies deeply in the pelvic cavity and is then a small sac, of an irregularly triangular form. As it becomes filled, it assumes a globular or ovoid form, rises up in the pelvic cavity, and when excessively distended, it may extend partly into the abdomen. When the urine is voided at normal intervals, the bladder, when filled, contains about a pint (nearly 500 c. c.) of liquid; but under pathological conditions it may become distended so as to contain ten or twelve pints (about 4 or 5 litres), and in some instances of obstruction it has been found to contain even more. The bladder is usually more capacious in the female than in the male.

The coats of the bladder are three in number. The external coat is simply a reflection of the peritoneum, covering the posterior portion completely, from the openings of the ureters to the summit, about one-third of the lateral portion and a small part of the anterior portion.

The middle or muscular coat consists of non-striated fibres, arranged in three tolerably distinct layers: The external muscular layer is composed of longitudinal fibres, which arise from parts adjacent to the neck, and pass anteriorly, posteriorly and laterally over the organ, so that when they are contracted they diminish its capacity chiefly by shortening its vertical diameter. The fibres of the external layer are of a pinkish hue, being much more highly colored than the other layers. The middle layer is formed of circular fibres, arranged, on the anterior surface of the bladder, in distinct bands at right angles to the superficial fibres. They are thinner and less strongly marked on the posterior and lateral surfaces. The internal layer is composed of pale fibres arranged in longitudinal fasciculi, the anterior and lateral bundles anastomosing with each other, as they descend toward the neck of the bladder, by oblique bands of communication, and the posterior bundles interlacing in every direction, forming an irregular plexus. Here they are not to be distinguished from the fibres of the middle layer. This is sometimes called the plexiform layer, and it gives to the interior of the bladder its reticulated appearance. This layer is continuous with the muscular fibres of the urachus, the ureters and the urethra.

The sphincter vesicæ is a band of non-striated fibres, about half an inch (12·7 mm.) in breadth and one-eighth of an inch (3·2 mm.) in thickness, embracing the neck of the bladder and the posterior half of the prostatic portion of the urethra. The tonic contraction of these fibres prevents the flow of urine, and during the ejaculation of the seminal fluid, it offers an obstruction to its passage into the bladder.

The mucous membrane of the bladder is smooth, rather pale, thick, and loosely adherent to the submucous tissue, except over the corpus trigonum. The epithelium is stratified and presents the same diversity in form as that observed in the pelvis of the kidney and the ureters; viz., the deeper cells are elongated and resemble columnar epithelium, while the cells on the surface are flattened. In the neck and fundus of the bladder, are a few mucous glands, some in the form of simple follicles and others collected to form glands of the simple racemose variety.

The corpus trigonum is a triangular body, lying just beneath the mucous membrane, at the base of the bladder, and extending from the urethra in front, to the openings of the ureters. It is composed of ordinary fibrous tissue, with a few elastic and muscular fibres. At the opening of the urethra, it presents a small, projecting fold of mucous membrane, which is sometimes called the uvula vesicæ. Over the whole of the surface of the trigone, the mucous membrane is very closely adherent, and it is never thrown into folds, even when the bladder is entirely empty.

The blood-vessels going to the bladder are ultimately distributed to its mucous membrane. They are not very abundant except at the fundus, where the mucous membrane is quite vascular. Lymphatics have been described as existing in the walls of the bladder, but Sappey has failed to demonstrate them in this situation. The nerves of the bladder are derived from the hypogastric plexus.

The urethra is provided with muscular fibres, and it is lined by a mucous membrane, the anatomy of which will be more fully considered in connection with the physiology of generation. In the female the epithelium of the urethra is like that of the bladder. In the male the epithelial cells are small, pale and of the columnar variety.

*Mechanism of the Discharge of Urine.*—In the human subject the urine is discharged into the pelves of the kidneys and the ureters by pressure due to the act of separation of fluid from the blood. Once discharged into the ureters, the course of the urine is determined in part by the *vis a tergo*, and in part, probably, by the action of the muscular coats of these canals. Müller has found that the ureters can be made to undergo a powerful local contraction by the application of a Faradic current; and Bernard has shown that this may be produced by stimulation of the anterior roots of the eleventh dorsal nerves.

When the urine has accumulated to a certain extent in the bladder, a peculiar sensation is felt which leads to the act for its expulsion. The intervals at which it is experienced are very variable. The urine is usually voided before retiring to rest and upon rising in the morning, and generally two or three times, in addition, during the day. The frequency of micturition, however, depends very much upon habit, upon the quantity of liquids ingested and upon the degree of activity of the skin.

Evacuation of the bladder is accomplished by the muscular walls of the organ itself, aided by contractions of the diaphragm and the abdominal muscles with certain muscles which operate upon the urethra, and it is accompanied by relaxation of the sphincter vesicæ. This act is at first voluntary, but once begun, it may be continued by the involuntary contraction of the bladder alone. During the first part of the process, the distended bladder is compressed by contraction of the diaphragm and the abdominal muscles; and this after a time excites the action of the bladder itself. A certain time usually elapses then before the urine begins to flow. When the bladder contracts, aided by the muscles of the abdomen and the diaphragm, the resistance of the sphincter is overcome, and a jet of urine flows from the urethra. All voluntary action may then cease for a time, and the bladder will nearly empty itself; but the force of the jet may be considerably increased by voluntary effort.

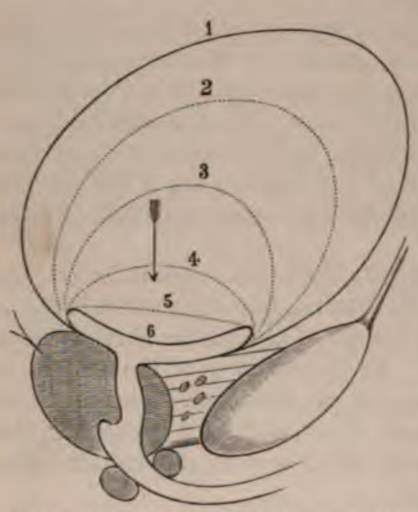

FIG. 118.—*Diagram showing the mechanism of micturition* (Küss.).

1, bladder distended with liquid; by the contraction of its walls it assumes successively the positions 2, 3, 4, 5; but the walls can not approach nearer the base without the aid of the abdominal muscles, which, by a voluntary effort, bring the summit to the position indicated by the line 6.

Toward the end of the expulsive act, when the quantity of liquid remaining in the bladder is small, the diaphragm and the abdominal muscles are again called into action, and there is a convulsive, interrupted discharge of the small quantity of urine that remains. At this time the impulse from the bladder, and, indeed, the influence of the abdominal muscles and diaphragm, are very slight, and the flow of urine along the urethra is aided by the contractions of its muscular walls and the action of some of the perineal muscles, the most efficient being the accelerator urinæ; but with all this muscular action, a few drops of urine generally remain in the male urethra after the act of urination has been accomplished. The process of evacuation of urine in the female is essentially the same as in the male, with the exception of the slight modifications due to differences in the direction and length of the urethra.

According to Budge, the influence of the nervous system on the bladder operates through the sympathetic; and he has described a centre in the spinal cord, which presides over the contractions of the lower part of the intestinal canal, the bladder and the vasa deferentia. This is called the genito-spinal centre, and it has been located, in experiments upon rabbits, in the spinal cord, at a point opposite the fourth lumbar vertebra. From this centre the nervous filaments pass through the sympathetic nerve, communicating with the ganglion which corresponds to the fifth lumbar vertebra.

## Properties and Composition of the Urine.

The color of the urine is very variable within the limits of health, and it depends to a considerable extent upon the character of the food, the quantity of drink and the activity of the skin. As a rule the color is yellowish or amber, with more or less of a reddish tint. The fluid is perfectly transparent, free from viscidity, and exhales, when first passed, a peculiar, aromatic odor, which is by no means disagreeable. Soon after the urine cools, it loses this peculiar odor and has the odor known as urinous. This odor remains until the liquid begins to undergo decomposition. The color and odor of the urine usually are modified by the same physiological conditions. When the fluid contains a large proportion of solid matters, the color is more intense and the urinous odor is more penetrating; and when its quantity is increased by an excess of water, the specific gravity is low, the color is pale and the odor is faint. The first urine passed in the morning, immediately after rising, usually is more intense in color than that passed during the day, and contains a relatively larger proportion of solids in solution.

The temperature of the urine at the moment of its emission, under physiological conditions, varies but a very small fraction of a degree from 100° Fahr. (37·78° C.). This estimate is the result of an extended series of observations, by Byasson, in 1868.

In estimating the total quantity of urine discharged in the twenty-four hours, it is important to take into consideration the specific gravity, as an indication of the amount of solid matter excreted by the kidneys. Variations in quantity constantly occur in health, depending upon the proportion of water; but the quantity of solid matters excreted is usually more nearly uniform. It must also be taken into account that differences in climate, habits of life, etc., in different countries, have an important influence upon the daily quantity of urine. Parkes collected the results of twenty-six series of observations made in America, England, France and Germany, and found the average daily quantity of urine in healthy male adults, between twenty and forty years of age, to be fifty-two and a half fluidounces (1,552·6 c. c.), the average quantity per hour being two and one-tenth fluidounces (62 c. c.). The extremes were thirty-five ounces and eighty-one ounces (1,035 and 2,395 c. c.). The average quantity may be assumed to be about fifty-one fluidounces (1,500 c. c.). The normal range of variation is between thirty and sixty ounces (about 900 and 1,775 c. c.). The conditions which lead to a diminution in the quantity of urine usually are more efficient in their operation than those which tend to an increase; and the range below the normal standard is rather wider than it is above. More urine usually is secreted during the day than at night. The quantity of water discharged by the kidneys in the twenty-four hours is a little greater in the female than in the male; but in the female the specific gravity is lower, and the quantity of solid constituents is relatively and absolutely less (Becquerel).

The specific gravity of the urine should be estimated in connection with the absolute quantity in the twenty-four hours. Those who assume that the daily quantity is about fifty-one ounces (1,500 c. c.), give the ordinary specific gravity of the mixed urine of the twenty-four hours as about 1020. The specific gravity is liable to the same variations as the proportion of water, and the density is increased as the water is diminished. The ordinary range of variation in specific gravity is between 1015 and 1025; but without positively indicating any pathological condition, it may be as low as 1005 or as high as 1030.

The reaction of the urine is acid in the carnivora and alkaline in the herbivora. In the human subject it usually is acid at the moment of its discharge from the bladder; although at certain times of the day it may be neutral or feebly alkaline, the reaction depending upon the character of the food. The acidity may be measured by neutralizing the urine with an alkali in a solution that has previously been graduated with a solution of oxalic acid of known strength; and the degree of acidity is usually expressed by calling it equivalent to so many grains of crystallized oxalic acid.

As the result of a large number of observations made by Vogel and under his direction, the total quantity of acid in the urine of the twenty-four hours in a healthy adult male is equal to between thirty and sixty grains (2 and 4 grammes) of oxalic acid. The hourly quantity in these observations was equal, in round numbers, to between one and a half and three grains (0·1 and 0·2 gramme) of acid. The proportion of acid was found to be very variable in the same person at different times of the day. The urine contains no free acid, but its acidity under an animal or a mixed diet depends upon the presence of acid salts, of which the principal one is acid sodium phosphate, with possibly a little acid calcium phosphate.

*Composition of the Urine.*—Regarding the excrementitious constituents of the urine as a measure, to a certain extent, of the general process of dissimilation, it is more important to recognize the quantities of these products discharged in a definite time than to learn simply their proportions in the urine; and in the following table of composition of the urine, the absolute quantities of its different constituents, excreted in twenty-four hours, have been given when practicable.

### COMPOSITION OF THE HUMAN URINE.

| | | | | |
|---|---|---|---|---|
| Water (in 24 hours, 27 to 50 fluidounces, 800 to 1,480 c. c.—Becquerel) | | 967·47 | to | 940·36 |
| Urea (in 24 hours, 355 to 463 grains, 23 to 30 grammes—Robin) | | 15·00 | " | 23·00 |
| Uric acid, accidental, or traces | | | | |
| Sodium urate, neutral and acid<br>Ammonium urate, neutral and acid (in small quantity)<br>Potassium urate<br>Calcium urate<br>Magnesium urate | (In 24 hours, 6 to 9 grs., 0·39 to 0·58 gramme, of uric acid—Becquerel—or 9 to 14 grs., 0·58 to 0·9 gramme, of urates, estimated as neutral urate of soda) | 1·00 | " | 1·60 |
| Sodium hippurate<br>Potassium hippurate<br>Calcium hippurate | (In 24 hours, about 7·5 grs., 0·486 gramme, of hippuric acid—Thudichum—equivalent to about 8·7 grs., 0·566 gramme, of sodium hippurate) | 1·00 | " | 1·40 |
| Sodium lactate<br>Potassium lactate<br>Calcium lactate | (Daily quantity not estimated) | 1·50 | " | 2·60 |
| Creatine<br>Creatinine | (In 24 hours, about 11·5 grains, 0·745 gramme, of both—Thudichum) | 1·60 | " | 3·00 |
| Calcium oxalate (daily quantity not estimated) | | traces | " | 1·10 |
| Xanthine | | not estimated. | | |
| Margarine, oleine and other fatty matters | | 0·10 | to | 0·20 |
| Sodium chloride (in 24 hours, about 154 grains, 10 grammes—Robin) | | 3·00 | " | 8·00 |
| Potassium chloride | | traces. | | |
| Ammonium chloride | | 1·50 | to | 2·20 |
| Sodium sulphate<br>Potassium sulphate<br>Calcium sulphate (traces) | (In 24 hours, 23 to 38 grains, 1·5 to 2·5 grammes, of sulphuric acid—Thudichum. About equal parts of sodium sulphate and potassium sulphate—Robin—equivalent to 22·5 to 37·5 grains, 1·45 to 2·43 grammes of each) | 3·00 | " | 7·00 |
| Sodium phosphate, neutral<br>Sodium phosphate, acid | (Daily quantity not estimated) | 2·50 | " | 4·30 |
| Magnesium phosphate (in 24 hours, 7·7 to 11·8 grains, 0·5 to 0·768 gramme—Neubauer) | | 0·50 | " | 1·00 |
| Calcium phosphate, acid<br>Calcium phosphate, basic | (In 24 hours, 4·7 to 5·7 grains, 0·307 to 0·372 gramme—Neubauer) | 0·20 | " | 1·30 |
| Ammonio-magnesian phosphate (daily quantity not estimated) | | 1·50 | " | 2·40 |
| (Daily excretion of phosphoric acid, about 56 grains, 3·629 grammes—Thudichum.) | | | | |
| Silicic acid | | 0·03 | " | 0·04 |
| Urochrome<br>Mucus from the bladder | | 0·10 | " | 0·50 |
| | | 1,000·00 | | 1,000·00 |

Proportion of solid constituents, 32·63 to 59·89 parts per 1,000.

*Gases of the Urine.* (Parts per 1,000, in volume.)

| | | | |
|---|---|---|---|
| Oxygen in solution | 0·90 | to | 1·00 |
| Nitrogen in solution | 7·00 | " | 10·00 |
| Carbon dioxide in solution | ·45 | " | 50·00 |

*Urea.*—As regards quantity, and probably as a measure of the activity of the general process of disassimilation, urea—$CO(NH_2)_2$—is the most important of the urinary constituents. Regarding the daily excretion of urea as a measure of the physiological wear of certain tissues, its consideration would come properly under the head of nutrition, in connection with other substances known to be the results of disassimilation; but it is convenient to treat of its general physiological properties and some of its variations in common with other excrementitious principles separated by the kidneys, in connection with the composition of the urine.

The formula for urea, showing the presence of a large proportion of nitrogen, would lead to the supposition that this substance is one of the products of the wear of the nitrogenized constituents of the body. It is found, under normal conditions, in the urine, the lymph and chyle, the blood, the sweat, the vitreous humor, and a trace in the saliva. Its presence has been demonstrated, also, in the substance of the healthy liver in both carnivorous and herbivorous animals; and it has been shown that it exists in minute quantity in the muscular juice (Zalesky). Under pathological conditions, urea finds its way into various other fluids, such as the secretion from the stomach, the serous fluids etc.

Urea is one of the few organic substances that have been produced artificially. In 1828, Wöhler obtained urea by adding ammonium sulphate to a solution of potassium cyanate. The products of this combination are potassium sulphate, with cyanic acid and ammonium in a form to constitute urea. Ammonium cyanate is isomeric with urea, and the change is effected by a re-arrangement of its elements. It has long been known that urea is readily convertible into ammonium carbonate; and ammonium carbonate, when heated in sealed tubes to the temperature at which urea begins to decompose, is converted into urea (Kolbe).

FIG. 119.—*Urea crystallized from an aqueous solution* (Funke).

Urea may readily be extracted from the urine, by processes fully described in works upon physiological chemistry; and its proportion may now easily be estimated by the various methods of volumetric analysis. It is not so easy, however, to separate it from the blood or from the substance of any of the tissues, on account of the difficulty in getting rid of other organic matters and the readiness with which it undergoes decomposition.

When perfectly pure, urea crystallizes in the form of long, four-sided, colorless and transparent prisms, which are without odor, neutral, and in taste resemble saltpetre. These crystals are very soluble in water and in alcohol, but they are entirely insoluble in ether. In its behavior with reagents, urea acts as a base, combining readily with certain acids, particularly nitric and oxalic. It also forms combinations with certain salts, such as mercuric oxide, sodium chloride etc. It exists in the economy in a state of watery solution, with perhaps a small portion modified by the presence of sodium chloride.

*Origin of Urea.*—It is now universally admitted by physiologists that urea is not formed in the kidneys but preëxists in the blood. It finds its way into the blood, in part directly from the tissues, and in part from the lymph, which contains a greater proportion of urea than is found in the blood itself. The quantity of urea in the blood is kept down by the eliminating action of the kidneys. Although a great part of the lymph is probably derived from the blood, it is not probable that the blood gives to the lymph all of the urea contained in the latter fluid; and it must be assumed that a part of the urea of the lymph passes from the tissues into the lymph-spaces and canals, although a certain quantity may be produced by the lymphatic glands.

As an outcome of many contradictory experiments and opinions on the subject, it must now be considered as proved that the liver produces urea in large quantity. If defibrinated blood be passed several times through a perfectly fresh liver, it gains urea. This observation, which was first made by Cyon, in 1870, has been repeatedly confirmed. In certain cases of structural disease of the liver, the excretion of urea is much diminished, and this substance may disappear from the urine. A number of cases illustrating this fact has been reported by Brouardel.

Assuming that urea is the most abundant and important of the nitrogenized excrementitious products—which is fully justified by physiological facts—it is difficult to avoid the conclusion that this substance represents, to a great extent, the disassimilation of the nitrogenized parts of the tissues, and necessarily the physiological wear of the muscular substance. The fact that urea exists in very minute quantity in the muscles—and some chemists state that it is absent—is probably due to its constant removal by the blood and lymph.

Uric acid, creatine, creatinine, xanthine, hypoxanthine, leucine, tyrosine and some other analogous substances are to be regarded as formations antecedent to urea, urea being the final and perfect excrementitious product.

It is convenient, in this connection, to consider the principal conditions which influence the formation and elimination of urea, or in order to compare this substance with certain constituents of food, the elimination of excrementitious nitrogen from the body.

*Influence of Ingesta upon the Composition of the Urine and upon the Elimination of Nitrogen.*—Water and other liquid ingesta usually increase the proportion of water in the urine and diminish its specific gravity. This is so marked after the ingestion of large quantities of liquids, that the urine passed under these conditions is sometimes spoken of by physiologists as the urina potus; but when an excess of water has been taken for purposes of experiment, the diet being carefully regulated, the absolute quantity of solid matters excreted is considerably increased. This is particularly marked as regards urea, but it is noticeable in the sulphates and phosphates, though not to any great extent in the chlorides. The results of experiments upon this point seem to show that water taken in excess increases the activity of disassimilation.

The ordinary meals increase the solid constituents of the urine, the most constant and uniform increase being in the proportion of urea. This, however, depends to a great extent upon the kind of food taken. The increase is usually noted during the first hour after a meal, and it attains its maximum at the third or fourth hour. The inorganic matters are increased as well as the excrementitious substances proper. The urine passed after food, has been called urina cibi, under the idea that it is to be distinguished from the urine supposed to be derived exclusively from disassimilation of the tissues, which is called the urina sanguinis.

It is an important question, to determine the influence of different kinds of food upon the composition of the urine, particularly the comparative effects of a nitrogenized and a non-nitrogenized diet. Lehmann has made a number of observations upon this point, and his results have been confirmed by many other physiologists. Without discussing fully all of these observations, it is sufficient to state that the ingestion of an excess of nitrogenized food always produced a great increase in the proportion of the nitrogenized constituents of the urine, particularly the urea. On a non-nitrogenized diet, the proportion of urea was found to be diminished more than one-half. The general results of the experiments of Lehmann are embodied in the following quotation:

"My experiments show that the amount of urea which is excreted is extremely dependent on the nature of the food which has been previously taken. On a purely animal diet, or on food very rich in nitrogen, there were often two-fifths more urea excreted than on a mixed diet; while, on a mixed diet, there was almost one-third more than on a purely vegetable diet; while, finally, on a non-nitrogenous diet, the amount of urea was less than half the quantity excreted during an ordinary mixed diet."

The influence of food is not absolutely confined to the period when any particular kind of food is taken, but is continued for many hours after a return to the ordinary diet.

With regard to the influence of food upon the inorganic constituents of the urine, it may be stated in general terms that the ingestion of mineral substances increases their proportion in the excretions.

There are certain articles which, when taken into the system, the diet being regular, seem to retard the process of disassimilation; or at least they diminish, in a marked manner, the quantity of matters excreted, particularly urea. Alcohol has a very decided influence of this kind. Its action may be modified by the presence of salts and other matters in the different alcoholic beverages, but in nearly all direct experiments, alcohol either taken under normal conditions of diet, when the diet is deficient or when it is in excess, diminishes the excretion of urea. The same may be stated in general terms of tea and coffee.

*Influence of Muscular Exercise upon the Elimination of Nitrogen.*—In all observations with regard to the influence of muscular exercise upon the elimination of nitrogen, account should be taken of the influence of diet; and those observations are most valuable which have given the proportion of nitrogen eliminated to the nitrogen of food. The observations of Fick and Wislicenus (1866) showed a diminution in the elimination of nitrogen during work; but during the time of the muscular work, no nitrogenized food was taken. The same conditions obtained in certain of the observations of Parkes. In a series of observations made in 1870 (Flint), on a person who walked 317½ miles (about 510 kilometres) in five consecutive days, the diet was normal, and the proportionate quantity of nitrogen was calculated for three periods of five days each, with the following results:

For the five days before the walk, with an average exercise of about eight miles (13 kilometres) daily, the nitrogen eliminated was 92·82 parts for 100 parts of nitrogen ingested. For the five days of the walk, for every hundred parts of nitrogen ingested, there were discharged 153·99 parts. For the five days after the walk, when there was hardly any exercise, for every hundred parts of nitrogen ingested, there were discharged 84·63 parts. During the walk, the nitrogen excreted was in direct ratio to the amount of work; and the excess of nitrogen eliminated, over the nitrogen of food, almost exactly corresponded with a calculation of the nitrogen of the muscular tissue consumed, as estimated from the loss of weight of the body. In 1876, a similar series of observations was made upon the same person by Pavy. In these observations, the subject of the experiment walked 450 miles (724·21 kilometres) in six consecutive days. During this period, the proportionate elimination of nitrogen was increased, but not to the extent observed in 1870. Similar results, although the experiments were made on a less extended scale, were obtained by North, in 1878. These results are opposed to the views of many physiologists, since the experiments of Fick and Wislicenus, who regard the elimination of nitrogen under ordinary conditions as dependent mainly upon the diet and not upon the muscular work performed. The observations of Voit, indeed, are favorable to this view.

Notwithstanding the results obtained by Fick and Wislicenus, Frankland, Haughton, Voit and others, the fact remains that excessively severe and prolonged muscular work increases the elimination of nitrogen over and above the quantity to be accounted for by the nitrogenized food taken. Actual observations (Flint, Pavy and others) are conclusive as regards this simple fact; but it is well known that muscular exercise largely increases the elimination of carbon dioxide and the consumption of oxygen. In exercise so violent as to produce dyspnœa, the distress in breathing is probably due to the impossibility of supplying by the lungs sufficient oxygen to meet the increased demand on the part of the muscular system, and the possible amount of muscular work is thereby limited.

The observations and conclusions of Oppenheim (1880) go far to harmonize the results obtained by different experimenters. Oppenheim concludes that muscular work, when not carried to the extent of producing shortness of breath or when moderate and extending over a considerable length of time, does not increase the elimination of urea; but that even less work, when violent and attended with shortness of breath, increases the discharge of urea. According to this view, moderate work draws upon the oxygen supplied to the body and at once largely increases the elimination of carbon dioxide; but the less active processes which result in the production of urea are not so promptly affected. Violent muscular work, however, or work which is excessively prolonged, consumes those parts of the tissues the destruction of which is represented by the discharge of urea. This view, if accepted, harmonizes the apparently contradictory experiments upon the influence of muscular work on the elimination of nitrogen.

The daily quantity of urea excreted is subject to very great variations. It is given in the table as 355 to 463 grains (23 to 30 grammes). This is less than the estimates frequently given; but when the quantity has been very large, it has generally depended upon an unusual amount of nitrogenized food, or the weight of the body has been above the average. Parkes has given the results of twenty-five different series of observations upon this point. The lowest estimate was 286·1 grains (18·24 grammes), and the highest, 688·4 grains (44·61 grammes).

*Uric Acid and its Compounds.*—Uric acid ($C_5H_4N_4O_3$) seldom if ever exists in a free state in normal urine. It is very insoluble, requiring fourteen to fifteen thousand times its volume of cold water or eighteen to nineteen hundred parts of boiling water for its solution. Its presence uncombined in the urine must be regarded as a pathological condition.

In normal urine, uric acid is combined with sodium, ammonium, potassium, calcium and magnesium. Of these combinations, the sodium urate

FIG. 120.—*Crystals of uric acid, obtained partly by the solution and subsequent precipitation of chemically pure acid, and partly by decomposition of the urates by nitric or acetic acid* (Funke).

FIG. 121.—*Sodium urate* (Funke).

and ammonium urate are by far the most important, and they constitute the great proportion of the urates, potassium, calcium and magnesium urates existing only in minute traces. Sodium urate is very much more abundant than ammonium urate. The union of uric acid with the bases is very feeble.

If from any cause the urine become excessively acid after its emission, a deposit of uric acid is likely to occur. The addition of a very small quantity of almost any acid is sufficient to decompose the urates, when the uric acid appears, after a few hours, in a crystalline form.

Uric acid, probably in combination with bases, was found in the substance of the liver in large quantity by Cloetta (1858), and his observations have been confirmed by recent authorities. The urates also exist in the blood in very small quantity and pass ready-formed into the urine. The fact that the urates exist in the liver has led to the opinion that this organ is the principal seat of the formation of uric acid (Meissner). However this may be, uric acid certainly is not formed in the kidneys, but is simply separated by these organs from the blood. Meissner did not succeed in finding uric acid in the muscular tissue, although the specimens were taken from animals in which he had found large quantities in the liver. The urates, particularly sodium urate, are products of disassimilation of the nitrogenized constituents of the body.

The daily excretion of uric acid, given in the table, is six to nine grains (0·39 to 0·58 gramme), the equivalent of nine to fourteen grains (0·58 to 0·9 gramme) of urates estimated as neutral sodium urate. Like urea, the proportion of the urates in the urine is subject to certain physiological variations.

*Hippuric Acid, Hippurates and Lactates.*—The compounds of hippuric acid ($C_9H_9NO_3$), which are so abundant in the urine of the herbivora, are now known to be constant constituents of the human urine. Hippuric acid is always to be found in the urine of children, but it is sometimes absent temporarily in the adult. The hippurates have been detected in the blood of the ox by Verdeil and Dolfuss, and they have since been found in the blood of the human subject. There can be scarcely any doubt that they pass, ready-formed, from the blood into the urine. As to the exact mode of origin of the hippurates, there is even less information than with regard to the origin of the other urinary constituents already considered. Experiments have shown that the proportion of hippuric acid in the urine is greatest after taking vegetable food; but it is found after a purely animal diet, and probably it also exists during fasting. The daily excretion of hippuric acid is about 7·5 grains (0·486 gramme), which is equivalent to about 8·7 grains (0·566 gramme) of sodium hippurate.

Hippuric acid itself, unlike uric acid, is soluble in water and in a mixture of hydrochloric acid. It requires six hundred parts of cold water for its solution, and a much smaller proportion of warm water. Under pathological conditions it is sometimes found free in solution in the urine.

Sodium, potassium and calcium lactates exist in considerable quantity in the normal urine. They are undoubtedly derived immediately from the blood, passing ready-formed into the urine, where they exist in simple watery solution. According to Robin, the lactates are formed in the muscles, in the substance of which they can readily be detected. Physiologists have little positive information with regard to the precise mode of formation of these salts. It is probable, however, that the lactic acid is the result of transformation of glucose. The lactic acid contained in the lactates extracted from the muscular substance is not identical with the acid resulting from the transformation of the sugars. The former have been called sarcolactates, and they contain one equivalent of water less than the ordinary lactates. The compounds of lactic acid in the urine are in the form of sarcolactates (Robin).

FIG. 122.—*Crystals of hippuric acid* (Funke).

*Creatine and Creatinine.*—Creatine ($C_4H_9N_3O_2$) and creatinine ($C_4H_7N_3O$) are probably identical in their relations to the general process of disassimilation, for one is easily converted into the other, out of the body, by very simple chemical means; and there is every reason to suppose that in the organism, they are the products of physiological wear of the same tissue or tissues. These substances have been found in the urine, blood, muscular tissue and brain. Scherer has demonstrated the presence of creatine in the amniotic fluid. By certain chemical manipulations, both creatine and creatinine may be converted into urea. Verdeil and Marcet have found both creatine and creatinine in the blood; and these substances are now regarded as excrementitious matters, taken from the tissues by the blood, to be eliminated by the kidneys.

Creatine has a bitter taste, is quite soluble in cold water (one part in seventy-five), and is much more soluble in hot water, from which it separates in

FIG. 123.—*Creatine, extracted from the muscular tissue, and crystallized from a hot, watery solution* (Funke).

FIG. 124.—*Creatinine, formed from creatine by digestion with hydrochloric acid, and crystallized from a hot, watery solution* (Funke).

a crystalline form on cooling. It is slightly soluble in alcohol and is insoluble in ether. A watery solution of creatine is neutral. It does not readily form combinations as a base; but it has lately been made to form crystalline compounds with some of the strong mineral acids, nitric, hydrochloric and sulphuric. When boiled for a long time with barium hydrate, it is changed into urea and sarcosine. When boiled with the strong acids, creatine loses an atom of water and is converted into creatinine. This change takes place very readily in decomposing urine, which contains neither urea nor creatine, but a large quantity of creatinine, when far advanced in putrefaction.

Creatinine is more soluble than creatine, and its watery solution has a strongly alkaline reaction. It is dissolved by eleven parts of cold water and is even more soluble in boiling water. It is slightly soluble in ether and is dissolved by one hundred parts of alcohol. This substance is one of the most powerful of the organic bases, readily forming crystalline combinations with a number of acids. According to Thudichum, creatine is the original excrementitious substance produced in the muscular substance, and creatinine is formed in the blood by a transformation of a portion of the creatine, somewhere between the muscles and the kidneys; "for, in the muscle, creatine has by far the preponderance over creatinine; in the urine, creatinine over creatine." The fact that creatine has been found in the brain would lead to the supposition that it is also one of the products of disassimilation of the nervous tissue.

The average daily excretion of creatine and creatinine was estimated by Thudichum at about 11·5 grains (0·745 gramme). Of this he estimated that 4·5 grains (0·292 gramme) consisted of creatine, and 7 grains (0·453 gramme) of creatinine.

*Calcium Oxalate.*—Calcium oxalate (oxalic acid, $C_2H_2O_4$) is not constantly present in normal human urine, although it may exist in certain quantity

FIG. 125.—*Crystals of calcium oxalate, deposited from the normal human urine, on the addition of ammonium oxalate to the urine* (Funke).

FIG. 126.—*Crystals of leucine* (Funke).

without indicating any pathological condition. It is exceedingly insoluble, and the appearance of its crystals, which are commonly in the form of small, regular octahedra, is quite characteristic. According to Neubauer, a small quantity may be retained in solution by the acid sodium phosphate in the urine. Calcium oxalate may find its way out of the system by the kidneys, after it has been taken with vegetable food or with certain medicinal substances. The ordinary rhubarb, or pie-plant, contains a large quantity of calcium oxalate, which, when this article is taken, will pass into the urine. It is probable, however, that a certain quantity may be formed in the organism.

Inasmuch as pathological facts have shown pretty conclusively that oxalic acid may appear in the system without having been introduced with the food, some physiologists have endeavored to show how it may originate from a change in certain other substances from which it can be produced artificially out of the body. One of the substances from which oxalic acid can be thus formed is uric acid. Woehler and Frerichs injected into the jugular vein of a dog a solution containing about twenty-three grains (1·5 gramme) of ammonium urate. In the urine taken a short time after, there was no deposit of uric acid, but there appeared a large number of crystals of calcium oxalate. The same result followed in the human subject, on the administration of sixty-seven grains (4·34 grammes) of ammonium urate by the mouth. These questions have more pathological than physiological importance; for the quantity of calcium oxalate in the normal urine is insignificant, and this salt does not seem to be connected with any of the well known processes of disassimilation.

*Xanthine, Hypoxanthine, Leucine, Tyrosine and Taurine.*—Traces of xanthine ($C_5H_4N_4O_2$) have been found in the normal human urine, but its pro-

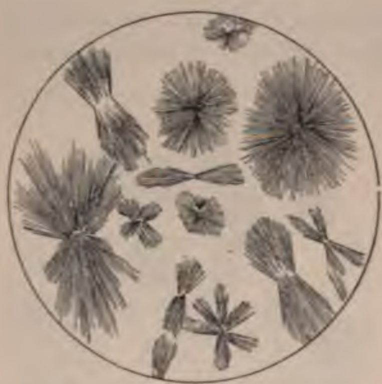

FIG. 127.—*Crystals of tyrosine* (Funke).

FIG. 128.—*Crystals of taurine* (Funke).

portion has not been estimated, and observers are as yet but imperfectly acquainted with its physiological relations. It has been found in the liver, spleen, thymus, pancreas, muscles and brain. It is insoluble in water but is soluble in both acid and alkaline fluids. Hypoxanthine ($C_5H_4N_4O$) has never been found in normal urine, although it exists in the muscles, liver, spleen and thymus. Leucine ($C_6H_{13}NO_2$) exists in the pancreas, salivary glands, thyroid, thymus, suprarenal capsules, lymphatic glands, liver, lungs, kidneys and the gray substance of the brain. It has never been detected in the normal urine. The same remarks apply to tyrosine ($C_9H_{11}NO_3$), although it is not so extensively distributed in the economy, to taurine ($C_2H_7NO_3S$) and to cystine

($C_3H_7NSO_2$). The last two, however, contain sulphur, and they may have peculiar physiological and pathological relations that are not at present understood.

These various substances are mentioned, although some of them have not been found in the normal urine, for the reason that there is evidently much to be learned with regard to the various products of disassimilation as they are represented by the composition of the urine. While some of them may not be actual constituents of the urine, but substances produced by the processes employed for their extraction, some, which have thus far been discovered only under pathological conditions, may yet be found in health, and they represent, perhaps, important physiological processes.

*Fatty Matters.*—Fat and fatty acids are said to exist in the normal urine in certain quantity. Their proportion, however, is small, and the mere fact of their presence, only, is of physiological interest.

*Inorganic Constituents of the Urine.*—It is by the kidneys that the greatest quantity and variety of inorganic salts are discharged from the organism; and it is probable that even now physiological chemists are not acquainted with the exact proportion and condition of all the constituents of this class found in the urine. In all the processes of nutrition, it is found that the inorganic constituents of the blood and tissues accompany the organic matters in their various transformations, although they are themselves unchanged. Indeed, the condition of union of inorganic with organic matters is so intimate, that they can not be completely separated without incineration. In view of these facts, it is evident that a certain proportion, at least, of the inorganic salts of the urine is derived from the tissues, of which, in combination with organic matters, they have formed a constituent part. As the kidneys frequently eliminate from the blood foreign matters taken into the system, and are capable sometimes of throwing off an excess of the normal constituents, which may be introduced into the circulation, it can readily be understood how a large proportion of some of the inorganic constituents of the urine may be derived from the food.

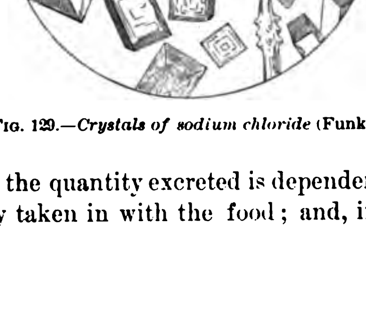

FIG. 129.—*Crystals of sodium chloride* (Funke).

*Chlorides.*—Almost all of the chlorine in the urine is in the form of sodium chloride, the quantity of potassium chloride being insignificant and not of any special physiological importance. By reference to the table of the composition of the urine, it is seen that the proportion of sodium chloride is subject to very great variations, the range being between three and eight parts per thousand. This at once suggests the idea that the quantity excreted is dependent to a considerable extent upon the quantity taken in with the food; and, indeed, it has been shown by direct observations that this is the fact. The proportion of sodium chloride in the blood seems to be tolerably constant; and any excess that may be introduced is thrown off, chiefly by the kidneys. As the chlorides are deposited with the organic matters in all the acts of nutrition, they are found to be eliminated constantly with the products of disassimilation of the nitrogenized parts, and their absence from the food does not completely arrest their discharge in the urine. According to Robin, by suppressing salt in the food, its daily excretion may be reduced to between thirty and forty-five grains (1·9 and 2·9 grammes). This quantity is less than that ordinarily contained in the ingesta, and under these conditions there is a gradual diminution in the general nutritive activity. In nearly all acute febrile disorders the chlorine in the urine rapidly diminishes and is frequently reduced to one-hundredth of the normal proportion. The quantity rapidly increases to the normal standard during convalescence. Most of the chlorides of the urine are in simple watery solution; but a certain proportion of sodium chloride exists in combination with urea.

The daily elimination of sodium chloride is about one hundred and fifty-four grains (10 grammes.) The great variations in its proportion in the urine, under different conditions of alimentation, etc., will explain the differences in the estimates given by various authorities.

*Sulphates.*—There is very little to be said regarding the sulphates, in addition to the general statements already made concerning the inorganic constituents of the urine. The proportion of these salts in the urine is very much greater than in the blood, in which there exist only about 0·28 of a part per thousand. Inasmuch as the proportion in the urine is three to seven parts per thousand, it seems probable that the kidneys eliminate these salts as fast as they find their way into the circulating fluid either from the food or from the tissues. Like other constituents derived in great part from the food, the normal variations in the proportion of sulphates in the urine are very great. It is unnecessary to consider in detail the variations in the quantity of sulphates discharged in the urine, depending upon the ingestion of different salts or upon diet, for all recorded observations have given the same results, and they show that the ingestion of sulphates in quantity is followed by a corresponding increase in the proportion eliminated.

Thudichum estimated the daily excretion of sulphuric acid at 23 to 38 grains (1·5 to 2·5 grammes). Assuming that the sulphates consist of about equal parts of potassium sulphate and sodium sulphate with traces of calcium sulphate, the quantity of salts would be 22·5 to 37·5 grains (1·46 to 2·23 grammes) of potassium sulphate, with an equal quantity of sodium sulphate.

*Phosphates.*—The urine contains phosphates in a variety of forms; but inasmuch as it is not known that any one of the different combinations possesses peculiar relations to the processes of disassimilation, as distinguished from the other phosphates, the phosphatic salts may be considered together.

The phosphates exist constantly in the urine and are derived in part from the food and in part from the tissues. Like other inorganic matters, they are united with the nitrogenized constituents of the organism, and when these are changed into excrementitious substances and are separated from the blood by the kidneys, they pass with them and are discharged from the body.

It is a question of some importance to consider how far the phosphates are derived from the tissues and what proportion comes directly from the food. All observers agree that the quantity of phosphates in the urine is in direct relation to the proportion in the food, and that an excess of phosphates taken into the stomach is immediately thrown off by the kidneys. It is a familiar fact, indeed, that the phosphates are deficient and the carbonates predominate in the urine of the herbivora, while the reverse obtains in the carnivora, and that variations, in this respect, in the urine, may be produced by feeding animals with different kinds of food. Deprivation of food diminishes the quantity of phosphates in the urine, but a certain proportion is discharged, which is derived exclusively from the tissues.

In connection with the fact that phosphorus exists in the nervous matter, it has been assumed that mental exertion is always attended with an increase in the elimination of phosphates; and this has been advanced to support the view that these salts are specially derived from disassimilation of the brain-substance. Experiments show that it is not alone the phosphates that are increased in quantity by mental work, but urea, the chlorides, sulphates and inorganic matters generally; and in point of fact, any physiological conditions which increase the proportion of nitrogenized excrementitious matters increase as well the elimination of inorganic salts. It can not be assumed, therefore, that the discharge of phosphates is specially connected with the activity of the brain. Little has been learned upon this point from pathology, for although many observations have been made upon the excretion of phosphoric acid in disease — Vogel having made about one thousand different analyses in various affections—no definite results have been obtained. From these facts it is seen that there is no physiological reason why the elimination of the phosphates should be specially connected with the disassimilation of any particular tissue or organ, especially as these salts in some form are universally distributed in the organism.

Observations have been made upon the hourly variations in the discharge of phosphoric acid at different times of the day; but these do not appear to bear any definite relation to known physiological conditions, not even to the process of digestion.

Of the different phosphatic salts of the urine, the most important are those in which the acid is combined with sodium. These exist in the form of the neutral and acid phosphates. The acid salt is supposed to be the source of the acidity of the urine at the moment of its emission. The so-called neutral salt is slightly alkaline. The proportion of the sodium phosphates in the urine is larger than that of any of the other phosphatic salts, but the daily quantity excreted has not been estimated. According to Robin, there always exists in the urine a small quantity of the ammonio-magnesian phosphate, but it never, in health, exists in sufficient quantity to form a crystalline deposit. The daily excretion of the phosphates is subject to great variations, but the average quantity of phosphoric acid excreted daily may be estimated at about fifty-six grains (3·629 grammes).

The urine contains, in addition to the inorganic salts that have been mentioned, a small quantity of silicic acid; but as far as is known, this has no physiological importance.

*Coloring Matter and Mucus.*—The peculiar color of the urine is due to the presence of a nitrogenized substance called urochrome. This is also called urohæmatine, uroxanthine and purpurine. There is no accurate account of its composition, and all that is known is that it contains carbon, oxygen, hydrogen and nitrogen, and probably iron. Although its exact chemical composition is not absolutely determined, its elements are supposed to be nearly the same as those of the coloring matter of the blood, the proportion of oxygen being much greater. These facts point to the probability of the formation of urochrome from hæmaglobine.

The quantity of coloring matter in the normal urine is very small. It is subject to considerable variation in disease, and almost always it is fixed by deposits and calculi of uric acid or the urates, giving them their peculiar color. This substance first makes its appearance in the urine and is probably formed in the kidneys. So little is known of its physiological or pathological relations to the organism, that it does not seem necessary to follow out all of the chemical details of its behavior in the presence of different reagents.

The normal urine always contains a small quantity of mucus, with more or less epithelium from the urinary passages and a few leucocytes. These form a faint cloud in the lower strata of healthy urine after a few hours' repose. The properties of the different kinds of mucus have already been considered. An important peculiarity, however, of the mucus contained in normal urine is that it does not seem to excite decomposition of the urea, and that the urine may remain for a long time in the bladder without undergoing putrefactive changes.

*Gases of the Urine.*—In the process of separation of the urine from the blood by the kidneys, a certain proportion of the gases in solution in the circulating fluid is also removed. For a long time, indeed, it has been known that the normal human urine contained different gases; but observations on this subject have been made by Morin (1864), in which the proportions of the free gases in solution have been accurately estimated. By using the method employed by Magnus in estimating the gases of the blood, Morin was able to extract about two and a half volumes of gas from a hundred parts of urine. He ascertained, however, that a certain quantity of gas remained in the urine and could not be extracted by the ordinary process. This was about one-fifth of the whole volume of gas. Adding this to the quantity of gas extracted, he obtained the following proportions to one litre of urine, in cubic centimetres (one part per thousand in volume):

| | |
|---|---|
| Oxygen | 0·824 |
| Nitrogen | 9·589 |
| Carbon dioxide | 19·620 |

These proportions represent the average of fifteen observations upon the urine secreted during the night.

The proportion of these gases was found by Morin to be subject to certain variations. For example, after the ingestion of a considerable quantity of water or any other liquid, the proportion of oxygen was considerably increased (from 0·824 to 1·024), and the carbon dioxide was diminished more than one-half. The most important variations, however, were in connection with muscular exercise. After walking a long distance, the exercise being taken both before and after eating, the quantity of carbon dioxide was found to be double that contained in the urine after repose. The proportion of oxygen was very slightly diminished, and the nitrogen was somewhat increased; but the variations of these gases were insignificant.

It is not probable that the kidneys are very important as eliminators of carbon dioxide, but it is certain that the presence of this gas in the urine assists in the solution of some of the saline constituents of this fluid, notably the phosphates.

*Water regarded as a Product of Excretion.*—It has been shown by indirect observations that a large proportion of the hydrogen introduced as an ingredient of food, about eighty-five per cent., is not accounted for by the hydrogen of the excreta. Direct observations have shown, also, that under certain conditions, an excess of water over that introduced with food and drink is discharged from the body. One of these conditions is abstinence from food (Flint, 1878). The elimination of water is very much increased by muscular work (Pettenkofer and Voit, 1868; Flint, 1879). These facts point to the actual production of water in the body by a union of oxygen with hydrogen.

While it is not certain that water is constantly produced in the body, there can be no doubt with regard to its formation under some conditions, and the oxidation of hydrogen is important as one of the factors in the production of animal heat. If a certain proportion of the water discharged by the lungs, skin and kidneys be regarded as a product of oxidation within the body, the relations which it bears to nutrition are probably the same as those of some of the excretions, especially carbon dioxide, and are subject to nearly the same laws. It has not been shown, however, that water is produced constantly, like those substances universally regarded as true excretions; and it gives rise to no direct toxic phenomena when retained in the system or when its production is diminished pathologically. Water also has important physiological uses, particularly as a solvent. Still, carbon dioxide, with which water may be compared as regards its mode of production, is not in itself poisonous, its retention in the blood simply interfering with the absorption of oxygen; and carbon dioxide probably is useful in increasing the solvent properties of the liquids of the organism. The relations of the formation of water in the body to the production of animal heat will be fully considered in connection with the physiology of nutrition and calorification.

*Variations in the Composition of the Urine.*—The urine not only represents, in its varied constituents, a great part of the physiological disintegration of the organism, but it contains matters evidently derived from the food. Its constitution is varying with every different condition of nutrition, with exercise, bodily and mental, with sleep, age, sex, diet, respiratory activity, the quantity of cutaneous exhalation, and, indeed, with every condition that affects any part of the system. There is no fluid in the body that presents such a variety of constituents as a constant condition, but in which the proportion of these constituents is so variable. It is for this reason that in the table of the composition of the urine, the ordinary limits of variation of its different constituents have been given; and it has been found necessary, in treating of the individual excrementitious products, to refer to some of the variations in their proportion in the urine.

*Variations with Age and Sex.*—There are decided differences in the composition of the urine at different periods of life and in the sexes. These undoubtedly depend in part upon the different conditions of nutrition and exercise and in part upon differences in the food. Although the quantities of excrementitious matters present great variations, their relations to the organism are not materially modified, except, perhaps, at an early age; and the influence of sex and age operates merely as these conditions affect the diet and the general habits of life.

It has been stated that urea does not exist in the urine of the fœtus; but in a specimen of urine taken from a still-born child delivered with forceps, examined by Elliot and Isaacs, the presence of urea was determined. Beale found urea in a specimen taken at the seventh month. Observations upon children between the ages of three and seven have shown that at this period of life, the urea excreted in proportion to the weight of the body is about double the quantity excreted in the adult. The chlorine in the urine of children is about three times the quantity in the adult; and the quantities of other solid matters are also greater. The quantity of water excreted by the kidneys in children, in proportion to the weight of the body, is very much greater than in the adult, being more than double. Between the ages of eight and eighteen years, the urinary excretion gradually approximates the standard in the adult. It has been observed that crystals of calcium oxalate are much more frequent in the urine of children between four and fourteen years of age than in the adult.

There are not many definite observations on record upon the composition of the urine in the later periods of life. It has been shown, however, that there is a decided diminution, at this time, in the excretion of urea, and that the absolute quantity of urine is somewhat less.

The absolute quantity of the urinary excretion in women is less than in men, and the same is true of the quantity in proportion to the weight of the body; still, the differences are not very marked, and the proportion of the urinary constituents being subject to modifications from the same causes as in men, the small deficiency, in the few direct observations on record, may be in part if not entirely explained by the fact that women usually perform less mental and physical work than men, and that their digestive system is generally not so active.

*Variations at Different Seasons and at Different Periods of the Day.*—The changes in the quantity and composition of the urine which may be directly referred to the conditions of digestion, temperature, sleep, exercise etc., have long been recognized by physiologists; but it is difficult so to separate these influences that the true modifying value of each can be fully appreciated. For example, there is nothing which produces such marked variations in the composition of the urine as the digestion of food. Under strictly physiological conditions, the modifying influence of digestion must always complicate observations upon the effects of exercise, sleep, season, period of the day etc.; and the urine is continually varying in health, with the physiological modifications in the various processes and conditions of life.

At different seasons of the year and in different climates, the urine presents certain variations in its quantity and composition. It seems necessary that a tolerably definite quantity of water should be discharged from the body at all times; and when the temperature or the hygrometric condition of the atmosphere is favorable to the action or the skin, as in a warm, dry climate, the quantity of water in the urine is diminished and its proportion of solid matters is correspondingly increased. On the other hand, the reverse obtains when the action of the skin is diminished from any cause.

At different times of the day, the urine presents certain important variations. It is evident that the specific gravity must be constantly varying with the relative proportions of water and of solid constituents. According to Dalton, the urine first discharged in the morning is dense and highly colored; that passed during the forenoon is pale and of a low specific gravity; and in the afternoon and evening it is again deeply colored, and its specific gravity is increased. The acidity is also subject to certain variations, which have already been mentioned.

*Influence of Mental Exertion.*—Although the influence of mental exertion upon the composition of the urine has not been very closely studied, the results of the investigations which have been made upon this subject are in many regards quite satisfactory. It is a matter of common remark that the secretion of urine is often modified to a considerable extent through the nervous system. Fear, anger, and various violent emotions, sometimes produce a sudden and copious secretion of urine containing a large proportion of water, and this is often observed in cases of hysteria. Intense mental exertion will occasionally produce the same result. In studying the influence of cerebral activity upon the composition of the urine, Byasson found that by mental exertion the quantity of urine was increased; the urea was also increased; the phosphoric acid was increased about one-third; the sulphuric acid was more than doubled; and the chlorine was nearly doubled.

The products of spontaneous decomposition of the urine have a certain chemical interest but are of no physiological importance.

# CHAPTER XIII.

## *USES OF THE LIVER—DUCTLESS GLANDS.*

Physiological anatomy of the liver—Distribution of the portal vein, the hepatic artery and the hepatic duct—Structure of a lobule of the liver—Arrangement of the bile-ducts in the lobules—Anatomy of the excretory biliary passages—Nerves and lymphatics of the liver—Mechanism of the secretion and discharge of bile—Quantity of bile—Uses of the bile—Properties and composition of the bile—Biliary salts—Cholesterine—Tests for bile—Excretory action of the liver—Formation of glycogen in the liver—Change of glycogen into sugar—Conditions which influence the quantity of sugar in the blood—Summary of the glycogenic action of the liver—Probable office of the ductless glands—Physiological anatomy of the spleen—Suprarenal capsules—Addison's disease—Thyroid gland—Myxœdema—Thymus—Pituitary body and pineal gland.

### Physiological Anatomy of the Liver.

The liver has several uses in the economy, which are more or less distinct from each other. It secretes bile, a fluid concerned in digestion and containing at least one excrementitious product. Another office is the formation of glycogen, in which it acts as a ductless gland.

It is unnecessary, in this connection, to dwell upon the ordinary descriptive anatomy of the liver. It is sufficient to state that it is situated just below the diaphragm, in the right hypochondriac region, and is the largest gland in the body, weighing, when moderately filled with blood, about four and a half pounds (2 kilos.). Its weight is somewhat variable, but in a person of ordinary adipose development, its proportion to the weight of the body is about as one to thirty-two. In early life the liver is relatively larger, its proportion to the weight of the body, in the new-born child, being as one to eighteen or twenty (Sappey).

The liver is covered externally by peritoneum, folds or duplicatures of this membrane being formed as it passes from the surface of the liver to the adjacent parts. These constitute four of the so-called ligaments that hold the liver in place. The proper coat is a thin but dense and resisting fibrous membrane, adherent to the substance of the organ, but detached without much difficulty, and very closely united to the peritoneum. This membrane is of variable thickness at different parts of the liver, being especially thin in the groove for the vena cava. At the transverse fissure, it surrounds the duct, blood-vessels and nerves, and it penetrates the substance of the organ in the form of a vagina, or sheath, investing the vessels, and branching with them. This membrane, as it ramifies in the substance of the liver, is called the capsule of Glisson. It will be more fully described in connection with the arrangement and distribution of the hepatic vessels.

The substance of the liver is made up of lobules, of an irregularly ovoid or rounded form, and about $\frac{1}{25}$ of an inch (1 mm.) in diameter. The space which separates these lobules is about one-quarter of the diameter of the lobule and is occupied by the blood-vessels, nerves and ramifications of the hepatic duct. In certain animals, the pig and the polar bear, the division of the hepatic substance can be readily made out with the naked eye; but in man and in most of the mammalia, the lobules are not so distinct, although their arrangement is essentially the same. The lobules are intimately connected with each other, and branches going to a number of different lobules are given off from the same interlobular vessels; but they are sufficiently distinct to represent, each one, the general anatomy of the secreting portion of the liver.

At the transverse fissure, the portal vein, collecting the blood from the abdominal organs, and the hepatic artery, which is a branch of the cœliac axis, penetrate the substance of the liver, with the hepatic duct, nerves and lymphatics, all enveloped in the fibrous vagina, or sheath, known as the capsule of Glisson. The portal vein is by far the larger of the two blood-vessels, and its caliber may be roughly estimated as eight to ten times that of the artery.

The vagina, or capsule of Glisson, is composed of fibrous tissue in the form of a dense membrane, closely adherent to the adjacent structure of the liver, and enveloping the vessels and nerves, to which it is attached by a loose, areolar tissue. The attachment of the blood-vessels to the sheath is so loose that the branches of the portal vein are collapsed when not filled with blood; presenting a striking contrast to the hepatic veins, which are closely adherent to the substance of the liver and remain open when they are cut across. This sheath is prolonged over the vessels as they branch and it follows them in their subdivisions. It varies considerably in thickness in different animals. In man and in the mammalia generally, it is rather thin, becoming more and more delicate as the vessels subdivide, and it is entirely lost before the vessels are distributed between the lobules.

The vessels distributed in the liver are the following:

The portal vein, the hepatic artery and the hepatic duct, passing in at the transverse fissure, to be distributed in the lobules. The blood-vessels are continuous in the lobules with the radicles of the hepatic veins. The duct is to be followed to its branches of origin in the lobules.

The hepatic veins; vessels that originate in the lobules, and collect the blood distributed in their substance by branches of the portal vein and of the hepatic artery.

*Branches of the Portal Vein, the Hepatic Artery and the Hepatic Duct.*—These vessels follow out the branches of the capsule of Glisson, become smaller and smaller, and they finally pass directly between the lobules. In their course, however, they send off lateral branches to the sheath, forming the so-called vaginal plexus. The arrangement of the vessels in the sheath is not in the form of a true anastomosing plexus, although branches pass from this so-called vaginal plexus between the lobules. These vessels do not anastomose or communicate with each other in the sheath.

The portal vein does not present any important peculiarity in its course from the transverse fissure to the interlobular spaces. It subdivides, enclosed in its sheath, until its small branches go directly between the lobules, and in its course, it sends branches to the sheath (vaginal vessels), which afterward go between the lobules. The hepatic artery has three sets of branches. As soon as it enters the sheath with the other vessels, it sends off minute branches (vasa vasorum), to the walls of the portal vein, to the larger branches of the artery itself, to the walls of the hepatic veins, and a very rich net-work of branches to the hepatic duct. In its course, the hepatic artery also sends branches to the capsule of Glisson (capsular branches), which, with branches of the portal vein, go to form the so-called vaginal plexus. From these vessels, a few arterial branches are given off, which pass between the lobules. The hepatic artery can not be followed beyond the interlobular vessels. The terminal branches of the hepatic artery are not directly connected with the radicles of the hepatic veins, but they empty into small branches of the portal vein within the capsule of Glisson.

FIG. 130.—*Lobules of the liver, interlobular vessels and intralobular veins* (Sappey).
1, 1, 1, 1, 3, 4, lobules; 2, 2, 2, 2, intralobular veins injected with white; 5, 5, 5, 5, 5, interlobular vessels filled with a dark injection.

*Interlobular Vessels.*—Branches of the portal vein, coming from the terminal ramifications of the vessel within the capsule and from the branches in the walls of the capsule, are distributed between the lobules, constituting the greatest part of the so-called interlobular plexus. These are situated between the lobules and surround them; each vessel, however, giving off branches to two or three lobules, and never to one alone. They do not anastomose, and consequently they are not in the form of a true plexus. The diameter of these interlobular vessels varies between $\frac{1}{1440}$ and $\frac{1}{720}$ of an inch (17 and 34 $\mu$). In this distribution, the blood-vessels are followed by branches of the duct, which are much fewer and smaller, measuring only $\frac{1}{2500}$ of an inch (10 $\mu$), and some, even, have been measured that are not more than $\frac{1}{3000}$ of an inch (8 $\mu$) in diameter.

*Lobular Vessels.*—From the interlobular veins, eight or ten branches are given off which penetrate the lobule. As the interlobular vessels are situated between different lobules, each one sends branches into two and sometimes three of these lobules; so that, as far as vascular supply is concerned, these divisions of the liver are never absolutely distinct.

After passing from the interlobular plexus into the lobules, the vessels immediately break up into an elongated net-work of capillaries, $\frac{1}{3000}$ to $\frac{1}{2200}$ of an inch (8 to 11 $\mu$) in diameter, which occupy the lobules with a true plexus. These vessels are very abundant. The blood, having been distributed in the lobules by this lobular plexus, is collected by three or four venous radicles into a single central vessel situated in the long axis of the lobule, called the intralobular vein. A single lobule, surrounded by an interlobular vessel, showing the lobular capillary plexus, and the central vein (the intralobular vein) cut across, is represented in Fig. 131.

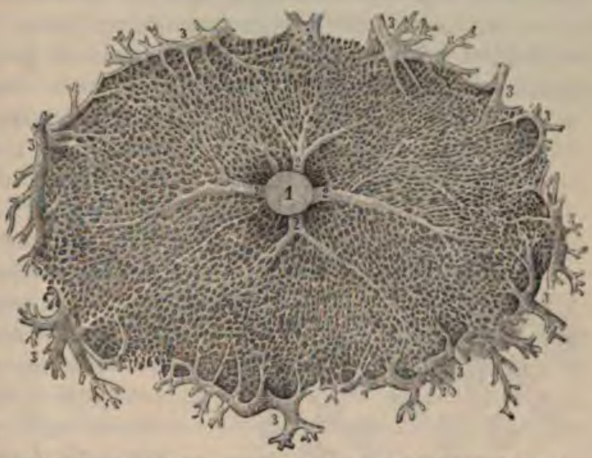


FIG. 131.—*Transverse section of a single hepatic lobule* (Sappey).
1, intralobular vein, cut across; 2, 2, 2, 2, afferent branches of the intralobular vein; 3, 3, 3, 3, 3, 3, 3, 3, 3, interlobular branches of the portal vein, with its capillary branches, forming the lobular plexus, extending to the radicles of the intralobular vein.

*Intralobular Veins.*—The capillaries of the lobules converge into three or four venous radicles (2, 2, 2, 2, in Fig. 131), which empty into a central vessel. This is the intralobular vein. If a liver be carefully injected from the hepatic veins, and if sections be made in various directions, it will be seen that the intralobular veins follow the long axis of the lobules, receiving vessels in their course, until they empty into a larger vessel situated at what may be called the base of the lobules. These latter are the sublobular veins. They collect the blood in the manner just described, from all parts of the liver, unite with others, becoming larger and larger, until finally they form the three hepatic veins, which discharge the blood from the liver into the vena cava ascendens.

The hepatic veins differ somewhat in their structure from other portions of the venous system. Their walls are thinner than those of the portal veins, they are not enclosed in a sheath, and they are very closely adherent to the hepatic tissue It has also been noted that the hepatic veins possess a well marked muscular tunic, very thin in man, but well developed in the pig, the ox and the horse, and composed of non-striated muscular fibres interlacing with each other in every direction.

In addition to the blood-vessels just described, the liver receives venous blood from vessels which have been called accessory portal veins, coming from the gastro-hepatic omentum, the surface of the gall-bladder, the diaphragm and from the anterior abdominal walls. These vessels penetrate at different points on the surface of the liver, and they may serve as derivatives, when the circulation through the portal vein is obstructed.

*Structure of a Lobule of the Liver.*—Each hepatic lobule, bounded and more or less distinctly separated from the others by the interlobular vessels, contains blood-vessels, radicles of the hepatic ducts and the so-called hepatic cells. The arrangement of the blood-vessels has just been described; but in all preparations made by artificial injection, the space occupied by the blood-vessels is exaggerated by excessive distention, and the difficulties in the study of the relations of the ducts and the liver-cells are thereby much increased.

*Hepatic Cells.*—If a scraping from the cut surface of a fresh liver be examined with a moderately high magnifying power, the field of view will be found filled with rounded, ovoid or irregularly polygonal cells, measuring $\frac{1}{1600}$ to $\frac{1}{1000}$ of an inch (16 to 25 $\mu$) in diameter. In their natural condition they are more frequently ovoid than polygonal; and when they have the latter form the corners are always rounded. These cells present one and occasionally two nuclei, sometimes with and sometimes without nucleoli. The presence of small, pigmentary granules gives to the cells a peculiar and characteristic appearance; and in addition, nearly all of them contain a few granules or small globules of fat. Sometimes the fatty and pigmentary granules are so abundant as to obscure the nuclei. The addition of acetic acid renders the cells pale and the nuclei become more distinct. The cells also contain more or less glycogen in the form of granules surrounding the nuclei.

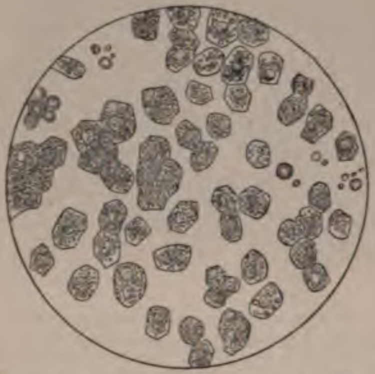

FIG. 132.—*Liver-cells from a human, fatty liver* (Funke).

*Arrangement of the Bile-ducts in the Lobules.*—In the substance of the lobules is a fine and regular net-work of vessels of nearly uniform size, about $\frac{1}{10000}$ of an inch (2 or 3 $\mu$) in diameter, which surround the liver-cells, each cell lying in a space bounded by inosculating branches of these canals. This plexus is entirely independent of the blood-vessels, and it seems to enclose in its meshes each individual cell, extending from the periphery of the lobule to the intralobular vein.

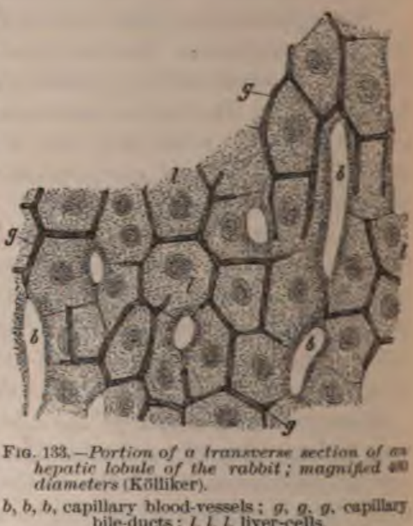


FIG. 133.—*Portion of a transverse section of an hepatic lobule of the rabbit; magnified 480 diameters* (Kölliker).
b, b, b, capillary blood-vessels; g, g, g, capillary bile-ducts; l, l, l, liver-cells.

The reticulated bile-ducts were discovered in the substance of the lobules, near their borders, by Gerlach, in 1848. It is evident, from an examination of his figures and description, that he succeeded in filling with injection that portion of the lobular net-work near the borders of the lobules, and he demonstrated the continuity of these vessels with the interlobular ducts; but he did not recognize the vessels nearer the centre of the lobule. It is now known that there are either canals or interspaces between the liver-cells in the lobules, and that these open into the interlobular hepatic ducts. It is still a question, however, whether these passages be simple spaces between the cells or true vessels lined with a membrane.

*Anatomy of the Excretory Biliary Passages.*—Between the lobules the ducts are very small, the smallest measuring about $\frac{1}{3000}$ of an inch (8 $\mu$) in diameter. They are composed of a delicate membrane lined with epithelium. The ducts larger than $\frac{1}{1200}$ of an inch (about 20 $\mu$) have a fibrous coat, formed of inelastic with a few elastic elements, and in the larger ducts, there are, in addition, a few non-striated muscular fibres. The epithelium lining these ducts is of the columnar variety, the cells gradually undergoing a transition from the pavement-form as the ducts increase in size. In the largest ducts there is a distinct mucous membrane with mucous glands.

Throughout the extent of the biliary passages, from the interlobular canals to the ductus choledochus, are little utricular or racemose glands, varying in size in different portions of the liver. These are situated, at short intervals, by the sides of the canals. The glands connected with the smallest ducts are simple follicles, $\frac{1}{800}$ to $\frac{1}{400}$ of an inch (31 to 62 $\mu$) long. The larger glands are formed of groups of these follicles, and they measure $\frac{1}{250}$ or $\frac{1}{100}$ of an inch (100 or 250 $\mu$) in diameter. The glands are only found connected with the ducts ramifying in the substance of the liver, and they do not exist in the hepatic, cystic and common ducts. They are composed of a homogeneous membrane, lined with small, pale cells of epithelium. If the ducts in the substance of the liver be isolated, they are found covered with these little groups of follicles and have the appearance of an ordinary racemose gland, except that the acini are relatively small and scattered. This appearance is represented in Fig. 134.

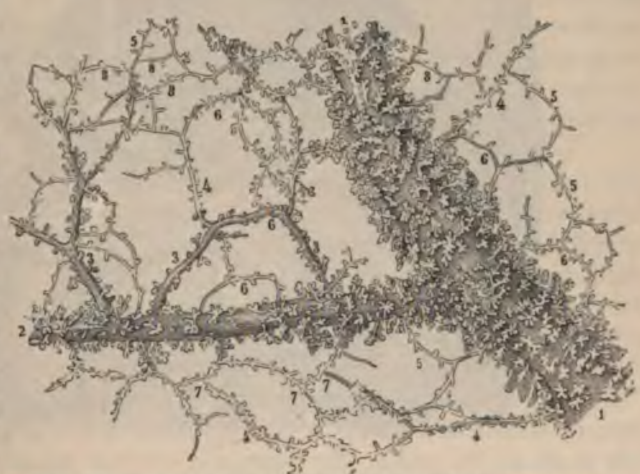

FIG. 134.—*Racemose glands attached to the biliary ducts of the pig; magnified 18 diameters* (Sappey).

1, 1, branch of an hepatic duct, with the surface almost entirely covered with racemose glands opening into its cavity; 2, branch in which the glands are smaller and less abundant; 3, 3, 3, branches of the duct with still simpler glands; 4, 4, 4, 4, biliary ducts with simple follicles attached; 5, 5, 5, 5, the same, with fewer follicles; 6, 6, 6, 6, 6, anastomoses in arches; 7, 7, 7, angular anastomoses; 8, 8, 8, 8, anastomoses by transverse branches.

The excretory biliary ducts, from the interlobular vessels to the point of emergence of the hepatic duct, present frequent anastomoses with each other in their course.

*Vasa Aberrantia.*—In the livers of old persons, and occasionally in the adult, certain vessels are found ramifying on the surface of the liver, but always opening into the biliary ducts, which have been called vasa aberrantia. These are never found in the fœtus or in children. They are appendages of the excretory system of the liver, and are analogous in their structure to the ducts, but are apparently hypertrophied, with thickened, fibrous walls, and present in their course irregular constrictions not found in the normal ducts. The racemose glands attached to them are always very much atrophied.

*Gall-bladder, Hepatic, Cystic and Common Ducts.*—The hepatic duct is formed by the union of two ducts, one from the right and the other from the left lobe of the liver. It is about an inch and a half (38 mm.) in length and joins at an acute angle with the cystic duct, to form the ductus communis choledochus. The common duct is about three inches (76 mm.) in length, of the diameter of a goose-quill, and it opens into the descending portion of the duodenum. It passes obliquely through the coats of the intestine, and opens into its cavity, in connection with the principal pancreatic


FIG. 135.—*Gall-bladder, hepatic, cystic and common ducts* (Sappey).
1, 2, 3, duodenum ; 4, 4, 5, 6, 7, 7, 8, pancreas and pancreatic ducts ; 9, 10, 11, 12, 13, liver ; 14, *gall-bladder ;* 15, *hepatic duct ;* 16, *cystic duct ;* 17, *common duct ;* 18, portal vein ; 19, branch from the cœliac axis ; 20, hepatic artery ; 21, coronary artery of the stomach ; 22, cardiac portion of the stomach ; 23, splenic artery ; 24, spleen ; 25, left kidney ; 26, right kidney ; 27, superior mesenteric artery and vein ; 28, inferior vena cava.

duct. The cystic duct is about an inch (25 mm.) in length, and is the smallest of the three canals.

The structure of these ducts is essentially the same. They have a proper coat formed of ordinary fibrous tissue, a few elastic fibres and non-striated muscular fibres. The muscular tissue is not sufficiently distinct to form a separate coat. The mucous membrane is always found tinged yellow with the bile, even in living animals. It is marked by a large number of minute excavations and is covered with cells of columnar epithelium. This membrane contains a large number of mucous glands.

The gall-bladder is an ovoid or pear-shaped sac, about four inches (10 centimetres) in length, one inch (25 mm.) in breadth at its widest portion, and capable of holding an ounce to an ounce and a half (30 to 45 c. c.) of fluid. Its fundus is covered entirely with peritoneum, but this membrane passes only over the lower surface of its body.

The proper coat of the gall-bladder is composed of ordinary fibrous tissue with a few elastic fibres. In some of the lower animals there is a distinct muscular coat, but a few scattered fibres only are found in the human subject. The mucous coat is of a yellowish color, with very small, interlacing folds which are very vascular. The mucous membrane of the gall-bladder has a general lining of columnar epithelium with a few goblet-cells. In the gall-bladder are found small, racemose glands, formed of four to eight follicles lodged in the submucous structure. These are essentially the same as the glands opening into the ducts in the substance of the liver, and they secrete a mucus which is mixed with the bile.

*Nerves and Lymphatics of the Liver.*—The nerves of the liver are derived from the pneumogastric, the phrenic, and the solar plexus of the sympathetic. The branches of the left pneumogastric penetrate with the portal vein, while the branches from the right pneumogastric, the phrenic and the sympathetic, surround the hepatic artery and the hepatic duct. All of these nerves penetrate at the transverse fissure and follow the blood-vessels in their distribution. They have not been traced farther than the final ramifications of the capsule of Glisson, and their exact mode of termination is unknown.

The lymphatics of the liver are very abundant. They are divided into two layers; the superficial layer, situated just beneath the serous membrane, and the deep layer. The superficial lymphatics from the under surface of the liver, and that portion of the deep lymphatics which follows the hepatic veins out of the liver, pass through the diaphragm and are connected with the thoracic glands. Some of the lymphatics from the superior, or convex surface join the deep vessels that emerge at the transverse fissure and pass into glands below the diaphragm, while others pass into the thoracic cavity.

The mode of origin of the lymphatics is peculiar. The superficial lymphatics are subperitoneal and are connected with spaces or canals in the general connective tissue of the liver. The deep lymphatics are supposed to originate by perivascular canals surrounding the blood-vessels of the lobules, which are connected with vessels in the walls of small branches of the hepatic and portal veins, afterward surrounding the larger vessels.

*Mechanism of the Secretion and Discharge of Bile.*—In its anatomy the liver differs greatly from other glandular organs, both secretory and excretory. The liver-cells are not enclosed in ducts, but are surrounded by a plexus of exceedingly small vessels which undoubtedly receive the bile as it is formed. The liver, also, is supplied with both venous and arterial blood, the venous blood largely predominating. In addition it is now recognized that the bile is necessary to intestinal digestion, that it contains excrementitious matters and that the cells constantly produce glycogen. The liver produces urea, which is excreted, however, chiefly by the kidneys. It may also effect certain changes in digested and foreign matters that are absorbed from the alimentary canal. As regards its varied uses, therefore, as well as in its anatomy, it has no analogue in the glandular system, and the mechanism of its action is necessarily complex.

As regards the secretion of bile, the only view that is consistent with actual knowledge is that this fluid is produced by the liver-cells and is taken up by the plexus of bile-ducts which surrounds these cells. The little glandular organs that are attached to the larger branches of the duct secrete mucus which gives the viscidity observed in the bile of some animals. The bile, indeed, is viscid in different animals in proportion to the development of these mucous glands; and in the rabbit, in which the glands do not exist, the bile has no viscidity (Sappey). The passage of excrementitious substances from the blood into the bile will be discussed in connection with the action of the liver as an organ of excretion, and the formation of glycogen will be considered in its proper place.

Of course the circulation of blood in the liver is a condition necessary to the secretion of bile. As regards the question of the production of bile from venous or arterial blood, it has been shown that the materials out of which the bile is formed may be supplied by either the hepatic artery or the portal vein. Bile is secreted after the hepatic artery has been tied, and also after the portal vein has been gradually obliterated, the hepatic artery being intact (Oré). Bile is produced in the liver from the blood distributed in its substance by the portal vein and the hepatic artery, and not from the blood of either of these vessels exclusively; and bile may continue to be secreted, if either one of these vessels be obliterated, provided the supply of blood be sufficient.

Some of the variations in the discharge of bile have been described in connection with the physiology of digestion; but although the bile is poured out much more abundantly during intestinal digestion than at other times, its production and discharge are constant. The bile is stored up in the gall-bladder to a considerable extent during the intervals of digestion. If an animal be killed at this time, the gall-bladder is always distended; but it is found empty, or nearly so, in animals killed during digestion.

The influence of the nervous system on the secretion of bile has been very little studied, and the question is one of great difficulty and obscurity. The liver is supplied very abundantly with nerves, both cerebro-spinal and sympathetic, and some observations have been made upon the influence of the nerves upon its glycogenic action; but with regard to the secretion of bile, there is little to be said beyond what has already been stated concerning the influence of the nervous system on other secretions.

The bile is discharged through the hepatic ducts like the secretion of any other gland. During digestion the fluid accumulated in the gall-bladder passes into the ductus communis, in part by contractions of its walls, and in part, probably, by compression exerted by the distended and congested digestive organs adjacent to it. It seems that this fluid, which is necessarily produced by the liver without intermission, separating from the blood certain excrementitious matters, is retained in the gall-bladder for use during digestion.

*Quantity of Bile.*—The estimates of the daily quantity of bile in the human subject must be merely approximate; and the ideas of physiologists on this point are derived chiefly from experiments upon the inferior animals. The most complete and reliable observations upon this subject are those of Bidder and Schmidt, which were made upon animals with a fistula into the gall-bladder, the ductus communis having been tied. These observers found great variations in the daily quantity in different classes of animals, the quantity in the carnivora being the smallest. Applying their results to the human subject, assuming that the amount is about equal to the quantity secreted by the carnivora, the daily secretion in a man weighing one hundred and forty pounds (63·5 kilos.) would be about two and a half pounds (1,134 grammes).

## Uses of the Bile.

The uses of the bile in digestion have already been fully described; but before considering its characters as an excretion, it will be necessary to study its general properties and composition.

*Properties and Composition of the Bile.*—The secretion as it comes directly from the liver is somewhat viscid; but after it has passed into the gall-bladder, its viscidity is much increased by a farther admixture of mucus.

The color of the bile is very variable within the limits of health. It may be of any shade between a dark, yellowish-green and a reddish-brown. It is semi-transparent, except when the color is very dark. In different classes of animals the variations in color are very great. In the pig it is bright-yellow; in the dog it is dark-brown; and in the ox it is greenish-yellow. As a rule the bile is dark-green in the carnivora and greenish-yellow in the herbivora.

The specific gravity of the human bile is 1,020 to 1,026. When the bile is perfectly fresh it is almost inodorous, but it readily undergoes putrefactive changes. It has a disagreeable and bitter taste. It is not coagulated by heat. When mixed with water and shaken, it becomes frothy, probably on account of the tenacious mucus and its saponaceous constituents.

It is generally stated that the bile is alkaline. This is true of the fluid discharged from the hepatic duct, although the alkalinity is not strongly marked; but the reaction varies after it has passed into the gall-bladder. Bernard found it sometimes acid and sometimes alkaline in the gall-bladder, in animals (dogs and rabbits) killed under various conditions; but many of these animals were suffering from the effects of severe operations. In the hepatic ducts the reaction is always alkaline; and there are no observations on human bile that show that the fluid is not alkaline in all of the biliary passages.

The epithelium of the biliary passages is strongly tinged with yellow, even in living animals. This is due to the facility with which the coloring matter of the bile stains the animal tissues. This is very well illustrated in icterus, when even a small quantity of this coloring matter finds its way into the circulation.

Perfectly normal and fresh bile, examined with the microscope, presents a certain quantity of mucus, the characters of which have already been described. There are no formed anatomical elements characteristic of this fluid. The fatty and coloring matters are in solution and not in the form of globules or granules.

COMPOSITION OF HUMAN BILE. (ROBIN.)

| | | | |
|---|---|---|---|
| Water | 916·00 | to | 819·00 |
| Sodium taurocholate | 56·50 | " | 106·00 |
| Sodium glycocholate | traces. | | |
| Cholesterine | 0·62 | to | 2·66 |
| Bilirubin | 14·00 | " | 30·00 |
| Lecithene; Palmitine, oleine and traces of soaps | 3·20 | " | 31·00 |
| Choline | traces. | | |
| Sodium chloride | 2·77 | to | 3·50 |
| Sodium phosphate | 1·60 | " | 2·50 |
| Potassium phosphate | 0·75 | " | 1·50 |
| Calcium phosphate | 0·50 | " | 1·65 |
| Magnesium phosphate | 0·45 | " | 0·60 |
| Salts of iron | 0·15 | " | 0·30 |
| Salts of manganese | traces | " | 0·12 |
| Silicic acid | 0·08 | " | 0·06 |
| Mucine | traces. | | |
| Loss | 3·43 | to | 1·21 |
| | 1,000·00 | | 1,000·00 |

There are no peculiarities in the composition of the bile, in respect to its inorganic constituents, which demand more than a passing mention. It contains no coagulable organic matters except mucine, and all of its constituents are simply solids in solution. The quantity of solid matter is very large, and the proportion of water is relatively small. Among the inorganic salts, sodium chloride exists in considerable quantity, with a large proportion of phosphates. There exist, also, salts of iron and of manganese, with a small quantity of silicic acid.

The fatty and saponaceous constituents demand hardly any more extended consideration. A small quantity of palmitine and oleine are held in solution, partly by the soaps, but chiefly by the sodium taurocholate. The fats sometimes exist in larger quantity, when they may be discovered in the form of globules. The proportion of soaps is very small. Lecithene ($C_{44}H_{90}NPO_9$) is a neutral, fatty substance extracted from the bile, and may be decomposed into phosphoric acid and glycerine. Choline ($C_5H_{15}NO_2$) is an alkaloid found in the bile in exceedingly minute quantity.

*Biliary Salts.*—In human bile the characteristic biliary salt is a combination of taurocholic acid ($C_{26}H_{45}NSO_7$) with sodium. A very small quantity of sodium exists in combination with glycocholic acid ($C_{26}H_{43}NO_6$). These two salts were discovered in the bile of the ox, by Strecker, in 1848. Sodium glycocholate exists in quantity in ox-gall. Both of these salts may be precipitated from an alcoholic extract of bile by an excess of ether. The taurocholate is precipitated in the form of dark, resinous drops which crystallize with difficulty. The glycocholate is readily crystallizable. The biliary salts are very soluble in water and in alcohol. Their reaction is neutral.

There can be no doubt that the biliary salts are products of secretion and are formed in the substance of the liver. In no instance have they ever been discovered in the blood in health; and although they present certain points of resemblance with some of the constituents of the urine, they have never been found in the excreta. In experiments made by Müller, Kunde, Lehmann and Moleschott, on frogs, in which the liver was removed and the animal survived several days—and in the observations of Moleschott, between two and three weeks—it was found impossible to determine the presence of the biliary salts in the blood. There is no reason, therefore, for supposing that these salts are products of disassimilation. Once discharged into the intestine, they undergo certain changes and can no longer be recognized by the usual tests; but experiments have shown that, changed or unchanged, they are absorbed with the products of digestion. They are probably concerned in the digestive action of the bile.

*Cholesterine.*—Cholesterine ($C_{26}H_{44}O$) is a normal constituent of various of the tissues and fluids of the body. Most authors state that it is found in the bile, blood, liver, nervous tissue, crystalline lens, meconium and fæcal matter. It is to be found in all these situations, with the exception of the fæces, where it does not exist normally, being transformed into stercorine in its passage down the intestinal canal.

In the fluids of the body cholesterine exists in solution; but by virtue of what constituents it is held in this condition, is a question that is not entirely settled. It is stated that the biliary salts have the power of holding cholesterine in solution in the bile, and that the small quantity of fatty acids contained in the blood holds it in solution in that fluid; but direct experiments on this point are wanting. In the nervous tissue and in the crystalline lens, it is united with the other substances which go to make up these parts. After it is discharged into the intestinal canal, when it is not changed into stercorine it is to be found in a crystalline form, as in the meconium, and in the fæces of certain animals in a state of hibernation. In pathological fluids and in tumors, it is found in a crystalline form and may be detected by microscopical examination.

Cholesterine is usually described as an alcohol, having many of the properties of the fats, but not that of saponification with the alkalies. It is neutral, inodorous, crystallizable, insoluble in water, soluble in ether and very soluble in hot alcohol, though sparingly soluble in cold alcohol. It is inflammable and burns with a bright flame. It is not attacked by the alkalies even after prolonged boiling. When treated with strong sulphuric acid it strikes a peculiar red color.

Cholesterine may easily and certainly be recognized under the microscope by the form of its crystals. They are rectangular or rhomboidal, very thin and transparent, of variable size, with distinct and generally regular borders, and frequently arranged in layers, with the borders of the lower strata showing through those which are superimposed. The plates of cholesterine are often marked by a cleavage at one corner, the lines running parallel to the borders. Frequently the plates are rectangular, and sometimes they are almost lozenge-shaped. Crystals of cholesterine melt at 293° Fahr. (145° C.), but they are formed again when the temperature falls below that point.

FIG. 136.—*Cholesterine extracted from the bile.*

The proportion of cholesterine in the bile is not very large. In the table, it is estimated at 0·62 to 2·66 parts per thousand. In a single examination of the human bile, the proportion was 0·618 of a part per thousand (Flint).

The origin and destination of cholesterine involve an office of the liver which has not been generally recognized by physiologists; and these questions will be considered specially, under the head of the excretory action of the liver.

*Bilirubin.*—The coloring matter of the bile, bilirubin ($C_{32}H_{36}N_4O_6$), bears a certain resemblance to the coloring matter of the blood and is supposed to be formed from it in the liver. It gives to the bile its peculiar tint and has the property of coloring the tissues with which it comes in contact. Whenever the flow of bile is obstructed for any considerable time, the coloring matter is absorbed by the blood and can be readily detected in the serum and in the urine. It also colors the skin and the conjunctiva. It is soluble in chloroform, by which it is distinguished from biliverdine, and forms soluble combinations with alkalies, in which form it is thought to exist in the bile. It probably is formed in the liver from the hæmoglobine of the red blood-corpuscles. When exposed to the air or to the influence of certain oxidizing agents, it assumes a greenish color and is changed into biliverdine. It is unnecessary to follow the various other changes produced by spontaneous decomposition or by the action of reagents.

*Tests for Bile.*—A simple test for bile-pigment is the following: A thin stratum of the liquid to be tested is placed upon a white surface, as a porcelain plate, and to this is added a drop of nitroso-nitric acid. If the coloring matter of the bile be present, a play of colors will be observed surrounding the drop of acid. The color will rapidly change from green to blue, red, orange, purple and finally to yellow. This test is applicable only to the coloring matter and does not detect the biliary salts.

A very delicate test for the biliary salts in a clear solution not containing albumen is what is known as Pettenkofer's test: To the suspected liquid are added a few drops of a strong solution of cane-sugar. Sulphuric acid is then slowly added, to the extent of about two-thirds of the bulk of the liquid. It is recommended to add the acid slowly, so that the temperature shall be but little raised. If a large quantity of the biliary salts be present, a red color shows itself almost immediately at the bottom of the test-tube, and this soon extends through the entire liquid, rapidly deepening until it becomes dark lake or purple. If the biliary matters exist in very small proportion, it may be several minutes before a red color makes its appearance, and the change to a purple is correspondingly slow, the whole process occupying fifteen to twenty minutes.

### Excretory Action of the Liver.

Although the liver produces a greater or less quantity of urea, this substance is discharged from the body chiefly in the urine and mere traces exist in the bile. The excretory action of the liver will be considered, in this connection, with reference to the bile itself. At the present day it is generally admitted that the bile is an excretion as well as a secretion; and this question has been fully discussed in connection with the physiology of digestion. The confusion that has arisen with regard to this point has been due to the fact that those who adopted the view that the bile was simply an excretion denied to it any digestive properties; while on the other hand, those who believed it to be concerned in digestion would not admit that it was an excretion. It will be useful, as bearing upon the probable office of the bile as an excretion, to apply to this fluid the general law of the distinctions between secretions and excretions.

Cells of glandular epithelium are constantly forming, out of materials furnished by the blood, the characteristic constituents of the true secreions; but these do not pre-exist in the blood, they appear first in the secretting organ, and they never accumulate in the system when the action of the secreting organ is disturbed. Again, the true secretions are not discharged from the body, but they have an office to perform in the economy, and are poured out by the glands intermittently, at the times when this office is called into action. As far as the biliary salts, sodium taurocholate and sodium glycocholate, are concerned, the bile corresponds entirely to the true secretions. These salts are formed in the liver, they do not pre-exist in the blood, and they do not accumulate in the blood when their formation in the liver is disturbed. The researches of Bidder and Schmidt and others have shown that although the biliary salts can not be detected in the blood or chyle coming from the intestine, they are not discharged in the fæces. These facts point to an important office of the bile as a secretion. It is true that the bile is discharged constantly, but during digestion its flow is very much more abundant than at any other time. It is pretty well established that during the intervals of the flow of the secretions, the glands are forming the materials of secretion, which are washed out, as it were, in the great afflux of blood which takes place during what has been called the activity of the gland.

The constant and invariable presence of cholesterine in the bile assimilates it in every regard to the excretions, of which the urine may be taken as the type. Cholesterine always exists in the blood and in certain of the tissues of the body. It is not produced in the substance of the liver, but is merely separated from the blood by this organ. It is constantly passed into the intestine, and is discharged, although in a modified form, in the fæces. Physiologists know of no office which it has to perform in the economy, any more than urea or any other of the excrementitious constituents of the urine. It accumulates in the blood in certain cases of organic disease of the liver and gives rise to symptoms of blood-poisoning.

*Origin of Cholesterine.*—Cholesterine exists in largest quantity in the substance of the brain and nerves. It is also found in the substance of the liver —probably in the bile contained in this organ—the crystalline lens and the spleen; but with these exceptions, it is found only in the nervous tissue and blood. It is either deposited in the nervous matter from the blood or it is formed in the brain and taken up by the blood. This is a question, however, which can be settled experimentally.

In a series of experiments made in 1862, it was invariably found that the proportion of cholesterine in the blood of the internal jugular vein and the femoral vein was greater than in the arterial blood. In experiments made on dogs not etherized, the blood of the jugular vein contained, in one instance 23·3 and in another 59·8 per cent. more cholesterine than the arterial blood of the same animals. The blood of the femoral vein contained about 6·3 per cent. more cholesterine than arterial blood. In three cases of hemiplegia, cholesterine was found in normal quantity in blood taken from the arm of the sound side, while blood from the paralyzed side contained no cholesterine (Flint).

These observations point to the production of cholesterine in the tissues; and the fact of its existence, under normal conditions, in the nervous tissue renders it probable that the chief seat of its production is the substance of the nerve-centres and nerves. The question of its formation in the spleen is one that has not been investigated.

In another series of experiments, it was shown that the blood lost cholesterine in passing through the liver. In one observation it was found that the arterial blood lost a little more than 23 per cent. and the portal blood, about 4½ per cent., in passing through the liver (Flint).

The portal blood, as it goes into the liver, contains but a small percentage of cholesterine over the blood of the hepatic vein, while the percentage in the arterial blood is large. The arterial blood is the mixed blood of the entire system; and as it probably passes through no organ which diminishes its cholesterine before it goes to the liver, it contains a quantity of this substance which must be removed. The portal blood, coming from a limited part of the system, contains less cholesterine, although it gives up a certain quantity. In the circulation in the liver, the portal system largely predominates and is necessary to other important actions of this organ, such as the production of glycogen; but soon after the portal vein enters the liver, its blood becomes mixed with that from the hepatic artery, and from this mixture the cholesterine is separated. It is necessary only that blood, containing a certain quantity of cholesterine, should come in contact with the bile-secreting cells, in order that this substance shall be separated. The fact that it is eliminated by the liver is proved with much less difficulty than that it is formed in the nervous system. In fact, its presence in the bile, and the necessity of its constant removal from the blood, consequent on its constant formation and absorption by this fluid, are almost sufficient in themselves to warrant the conclusion that it is eliminated by the liver.

In treating of the composition of the fæces, the changes which the cholesterine of the bile undergoes in its passages down the intestinal canal have been so fully considered that it is not necessary to refer to this portion of the subject again. But one examination only was made of the quantity of stercorine contained in the daily fæcal evacuation; and assuming that the quantity of cholesterine excreted by the liver is equal to the stercorine found in the evacuations, the quantity in twenty-four hours is about ten and a half grains (0·68 gramme). This corresponds with the estimates of the daily quantity of cholesterine excreted, calculated from its proportion in the bile and the estimated daily quantity of bile produced by the liver.

To complete the chain of the evidence leading to the conclusion that cholesterine is an excrementitious product which is formed in certain of the tissues and eliminated by the liver, it is necessary only to show that it may accumulate in the blood when the eliminating action of the liver is interrupted.

In a case of simple jaundice from duodenitis, in which there was no great disturbance of the system, a specimen of blood taken from the arm presented undoubted evidences of the coloring matter of the bile, but the proportion of cholesterine was not increased, being only 0·508 of a part per thousand. The fæces contained a large proportion of saponifiable fat, but no cholesterine or stercorine.

In a case of cirrhosis with jaundice, there was ascites, with great general prostration. This patient died a few days after the blood and fæces had been examined, and the liver was found in a condition of cirrhosis, with the liver-cells shrunken and the gall-bladder contracted. In this case the blood contained 1·85 of a part of cholesterine per thousand, more than double the largest quantity found in health. The fæces contained a small quantity of stercorine.

Inasmuch as cases frequently present themselves in which there are evidences of cirrhosis of the liver with little if any constitutional disturbance, while others are attended with grave nervous symptoms, it seemed an interesting question to determine whether it be possible for cholesterine to accumulate in the blood without the ordinary evidence of jaundice. An opportunity occurred of examining the blood in two strongly contrasted cases of cirrhosis, in neither of which was there jaundice. One of these patients had been tapped repeatedly—about thirty times—but the ascites was the only troublesome symptom and the general health was little impaired. In this case the proportion of cholesterine in the blood was only 0·246 of a part per thousand, considerably below the quantity ordinarily found in health. The other patient had cirrhosis, but he was confined to the bed and was very feeble. The proportion of cholesterine in the blood in this case was 0·922 of a part per thousand, a little above the largest proportion found in health. A few other pathological observations of this kind are on record. Picot, in 1872, reported a fatal case of "grave jaundice," in which he determined a great increase in the quantity of cholesterine in the blood, the proportion being 1·804 per 1000.

It is probable that organic disease of the liver, accompanied with grave symptoms generally affecting the nervous system, does not differ in its pathology from cases of simple jaundice in the fact of retention of the biliary salts in the blood; but these grave symptoms, it is more than probable, are due to a deficiency in the elimination of cholesterine and its consequent accumulation in the system. Like the accumulation of urea in structural disease of the kidney, this produces blood-poisoning; and this condition may be characterized by the name Cholesteræmia, a term expressing a pathological condition, but at the same time indicating the physiological relations of cholesterine.

Koloman Müller, in 1873, succeeded in injecting cholesterine into the blood-vessels without producing any effects due to mechanical obstruction of the circulation. He made a preparation by rubbing cholesterine with glycerine and mixing the mass with soap and water. He injected into the veins of dogs, 2·16 fluidounces (about 64 c. c.) of this solution, containing about 69 grains (4·5 grammes) of cholesterine. In five experiments of this kind, he produced a complete representation of the phenomena of "grave jaundice."

In view of all these facts, an excretory action of the liver, involving the separation of cholesterine from the blood and its discharge in the fæces in the form of stercorine, must be regarded as established, as well as the existence of cholesteræmia as a definite pathological condition.

### Formation of Glycogen in the Liver.

In addition to the uses of the liver already described, this organ constantly produces in health a substance resembling starch, called glycogen, which is converted into glucose and is carried into the circulation by the hepatic veins. In this way the liver acts as a ductless gland, glycogen being formed by the liver-cells in precisely the manner that the various constituents of the secretions are produced by other glands. The discovery of this, which was first called the sugar-producing office of the liver, was made by Bernard, in 1848. During the present century there have been few discoveries which have attracted so much attention, and Bernard's experiments have been repeated and extended by physiologists in different parts of the world. In 1857, Bernard discovered glycogen in the liver and showed that the production of this substance precedes the formation of sugar. In studying, then, the mechanism of sugar-production in animals, it will be necessary to begin with the physiological history of glycogen.

Glycogen ($C_6H_{10}O_5$) belongs to the class of carbohydrates and is isomeric with starch. It is readily converted into glucose ($C_6H_{12}O_6$). In nearly all regards it has the properties of starch, but it gives a deep red color with iodine instead of a blue. In the liver-cells it exists in the form of amorphous granules surrounding the nuclei. It may be extracted from a decoction of the liver-substance, by precipitating the albuminoids by adding alternately dilute hydrochloric acid and potassio-mercuric iodide, filtering and treating the filtrate with an excess of alcohol. The alcoholic precipitate, washed with alcohol and dried rapidly, is in the form of a white powder, which will keep indefinitely. In the adult, glycogen is most abundant in the liver; but it has been found in small quantity in the muscular substance, in cartilage and in certain cells in process of development. In the early months of fœtal life it exists in nearly all the tissues. It is found, also, in cells attached to the villi of the placenta.

The most important of the conditions which influence the quantity of glycogen in the liver relate to alimentation and digestion. The liver always contains more glycogen during digestion than in fasting animals. After a few days of starvation, glycogen may almost or quite disappear from the liver. This also occurs in animals fed for a time exclusively with fats, and the quantity is diminished by a purely albuminous diet as contrasted with a mixed diet. Still, as was shown by Bernard, glycogen is invariably present in the livers of healthy carnivorous animals that have always been fed with meat alone.

A very great increase in the quantity of glycogen in the liver is produced by feeding animals largely with carbohydrates. Not only are the starches apparently stored up for a time in the form of glycogen in the liver, but sugars seem to undergo a change into glycogen which accumulates in the liver. This is to be expected, as the starches are changed into sugar before they are absorbed, and all the carbohydrates behave in the same way as regards general nutrition. Very abundant alimentation with carbohydrates sometimes produces a temporary diabetes, the quantity of sugar in the blood increasing to such an extent that sugar is discharged in the urine. This is due either to the passage of a certain quantity of sugar unchanged through the liver or to an excessive formation of glycogen, which is more actively changed into sugar than under normal conditions.

As far as regards the influence of alimentation upon the formation of glycogen, it seems probable that in the herbivora and in man the chief source of hepatic glycogen is the class of alimentary substances called carbohydrates; but the fact that glycogen exists in the livers of the carnivora, and probably in man, under a nitrogenized diet, shows that the liver is capable of forming glycogen from the albuminoids.

*Change of Glycogen into Sugar.*—It is almost certain that the liver does not contain sugar during life. Many years ago (1858) this fact was recognized by Pavy, and it has since been confirmed by other physiologists. Pavy, however, assumed that there was no such thing as sugar-formation by the liver, under absolutely normal conditions. He regarded the sugar found in the substance of the liver and in the blood of the hepatic veins as due to post-mortem action, and his observations seemed to be directly opposed to those of Bernard. The views of these two observers and their followers seemed to be harmonized by a series of experiments made in 1868. If the abdomen of a dog, perfectly quiet and not under the influence of an anæsthetic, be opened, and a portion of the liver be excised, rinsed in cold water and rapidly cut up into boiling water, the extract will show no reaction with Fehling's test for sugar. In one experiment, in which twenty-eight seconds elapsed between the time of opening the abdomen and the action of the boiling water, the reaction with Fehling's test was doubtful. In an experiment in which the time was only ten seconds, there was no trace of sugar in the extract from the liver (Flint). Dalton, however, in 1871, found small quantities of sugar in extracts of portions of liver taken from an animal in an average time of 6¼ seconds; but it is possible that the sugar may have been in blood retained in the liver. All observers, however, are now agreed that sugar is formed in the liver very rapidly after death.

If the view be correct, that the glycogen of the liver is being constantly transformed into sugar during life, and that this sugar is carried away in the blood-current, as fast as it is formed, sugar would not necessarily be contained in the liver under normal conditions; and there is no actual antagonism between the results obtained by Bernard and the fact that sugar itself is not a normal constituent of the liver, as is asserted by Pavy, McDonnell, Meissner, Ritter and others.

If the liver be washed by a stream of water passed through its vessels until it is free from sugar, and if it be kept at the temperature of the body for a few hours, sugar will appear in abundance (Bernard, 1855). This is due to a conversion of the glycogen of the liver into sugar by a ferment, which has been extracted and isolated by Bernard and others by a process analogous to that by which similar ferments have been extracted from the saliva and the pancreatic juice. This ferment probably exists originally in the liver and does not appear first in the blood.

The question of the transformation of glycogen into sugar during life depends upon the comparative quantities of sugar in the blood going to and coming from the liver. Bernard always found sugar in quantity in the blood of the hepatic veins taken immediately after death, and it exists in blood drawn during life by a catheter introduced into the right cavities of the heart; while in the carnivora, under a purely animal diet, no sugar is contained in the blood of the portal system. The normal blood contains, perhaps, a small quantity of sugar—0·5 to 1 part per 1,000—but the proportion is always greater in the blood of the hepatic veins.

The characters of animal sugar do not materially differ from those of glucose, except that it ferments more readily and is destroyed in the system with great facility. This property of the sugar which results from the glycogen formed in the liver is probably of great importance. The sugar which results from digestion is all carried to the liver. Here it is changed into glycogen; and it is probable that without this change into glycogen and its subsequent transformation into what is called liver-sugar, it is not perfectly adapted to the purposes of nutrition. In many cases of diabetes, a possible explanation of the glycosuria is that the carbohydrates pass unchanged into the vena cava and do not undergo the changes which take place normally in the liver, at the same time being received into the general circulation suddenly and in large quantity, instead of gradually, as when they are changed into glycogen and afterward into liver-sugar. When an excess of sugar finds its way into the blood, it is probable that the liver, under normal conditions, retains it for a time in the form of glycogen.

The sugar which is discharged into the venous system by the hepatic veins is usually lost in the passage of the blood through the lungs. The question of the final destination of sugar will be taken up again in connection with the physiology of nutrition.

*Conditions which influence the Quantity of Sugar in the Blood.*—It is probable that disturbances of the circulation in the liver are the most important conditions influencing the discharge of sugar by the hepatic veins, and these operate mainly through the nervous system.

FIG. 137. — *Instrument for puncturing the floor of the fourth ventricle* (Bernard).

The most remarkable experiment upon the influence of the nervous system on the liver is the one in which artificial diabetes is produced by irritation of the floor of the fourth ventricle (Bernard). This operation is not difficult. The instrument used is a delicate stilet, with a flat, cutting extremity, and a small, projecting point about $\frac{1}{25}$ of an inch (1 mm.) long. In performing the operation upon a rabbit, the head of the animal is firmly held in the left hand, and the skull is penetrated in the median line, just behind the superior occipital protuberance. This can easily be done by a few lateral movements of the instrument. Once within the cranium, the instrument is passed obliquely downward and forward, so as to cross an imaginary line drawn between the two auditory canals, until its point reaches the basilar process of the occipital bone. The point then penetrates the medulla oblongata, between the roots of the auditory nerves and the pneumogastrics, and by its projection it serves to protect the nervous centre from more serious injury from the cutting edge. The instrument is then carefully withdrawn and the operation is completed. This experiment is almost painless, and it is not desirable to administer an anæsthetic, as this, in itself, would disturb the glycogenic process. The urine may be drawn before the operation, by pressing the lower part of the abdomen, taking care not to allow the bladder to pass up above the point of pressure, and it will be found turbid, alkaline and without sugar. In one or two hours after the operation, the urine will have become clear and acid, and it will react readily with any of the copper-tests. When this operation is performed without injuring the adjacent organs, the presence of sugar in the urine is temporary, and the next day the secretion will have returned to its normal condition. The production of diabetes in this way, in animals, is important in its relations to certain cases of the disease in the human subject, in which the affection is traumatic and directly attributable to injury near the medulla. Its mechanism is difficult to explain. The irritation is not propagated through the pneumogastric nerves, for the experiment succeeds after both of these nerves have been divided; nevertheless, the pneumogastrics have an important influence upon glycogenesis. If both of these nerves be divided in the neck, in a few hours or days, depending upon the length of time that the animal survives the operation, no sugar is to be found in the liver, and there is reason to believe that the glycogenic action has been arrested. After division of the nerves in the neck, stimulation of their peripheral ends does not affect the production of sugar; but stimulation of the central ends produces an impression which is conveyed to the nervous centre, is reflected to the liver and gives rise to an increased production of sugar.


FIG. 138.—*Section of the head of a rabbit, showing the operation of puncturing the floor of the fourth ventricle* (Bernard).

*a*, cerebellum; *b*, origin of the seventh pair of nerves; *c*, spinal cord; *d*, origin of the pneumogastric; *e*, opening of entrance of the instrument into the cranial cavity; *f*, instrument; *g*, fifth pair of nerves; *h*, auditory canal; *i*, extremity of the instrument upon the spinal cord, after it has penetrated the cerebellum; *k*, occipital venous sinus; *l*, tubercula quadrigemina; *m*, cerebrum; *n*, section of the atlas.

With regard to the influence of the sympathetic nerves upon glycogenic action, there have been few if any experiments which lead to conclusions of any great value.

It has been observed that the inhalation of anæsthetics and irritating vapors produces temporary diabetes; and this has been attributed to an irritation conveyed by the pneumogastrics to the nerve-centre, and reflected, in the form of a stimulus, to the liver. It is for this reason that the administration of anæsthetics should be avoided in all accurate experiments on glycogenic action.

The following summary expresses what is known with regard to the production of glycogen by the liver and its conversion into sugar:

A substance exists in the healthy liver, which is readily convertible into sugar; and inasmuch as this is changed into sugar during life, the sugar being washed away by the blood passing through the liver, it is proper to call it glycogen, or sugar-forming matter.

The liver has a glycogenic action, which consists in the constant formation of sugar out of the glycogen, the sugar being carried away by the blood of the hepatic veins, which always contains sugar in a certain proportion. This production of sugar takes place in the carnivora, as well as in those animals that take sugar and starch as food; and it is to a certain extent independent of the kind of food taken.

During life the liver contains glycogen only and no sugar, because the blood which is constantly passing through this organ washes out the sugar as fast as it is formed; but after death or when the circulation is interfered with, the transformation of glycogen into sugar continues. The sugar is not removed under these conditions, and it can then be detected in the substance of the liver.

The liver serves as a receptacle for the carbohydrates, which, under normal conditions of alimentation and nutrition, are all converted into glycogen. The glycogen is then converted into sugar, which is supplied to the system as the nutritive requirements demand.

In addition to the varied uses of the liver which have been described, it is thought that this organ either arrests or in some way influences the condition of certain foreign and poisonous substances which may be absorbed from the alimentary canal; but a study of this action does not properly belong to physiology.

## Ductless Glands.

Certain organs in the body, with a structure resembling, in some regards, the true glands, but without excretory ducts, have long been the subject of physiological speculation; and the most extravagant notions concerning their uses have prevailed in the early history of physiology. The discovery of the action of the liver, which consists in modifications in the composition of the blood passing through its substance, has foreshadowed the probable mode of action of the ductless glands; for as far as the production of glycogen is concerned, the liver belongs to this class. Indeed, the supposition that the ductless glands effect certain changes in the blood is now regarded by physiologists as the most reasonable of the many theories that have been entertained concerning their uses in the economy. Under this idea, these organs have been called blood-glands or vascular glands. Under the head of ductless glands, are classed the spleen, the suprarenal capsules, the thyroid gland, the thymus, and sometimes the pituitary body and the pineal gland.

## Physiological Anatomy of the Spleen.

The spleen is situated in the left hypochondriac region, next the cardiac extremity of the stomach. Its color is a dark bluish-red and its consistence is rather soft and friable. It is shaped somewhat like the tongue of a dog, presenting above, a rather thickened extremity, which is in relation with the diaphragm, and below, a pointed extremity, in relation with the transverse colon. Its external surface is convex. Its internal surface is concave, presenting a vertical fissure, the hilum, which gives passage to the vessels and nerves. It is connected with the stomach by the gastro-splenic omentum and is still farther fixed by a fold of peritoneum passing to the diaphragm. It is about five inches (127 mm.) in length, three to four inches (75 to 100 mm.) in breadth, and a little more than an inch (25·4 mm.) in thickness. Its weight is six to seven ounces (170 to 198 grammes). In the adult it attains its maximum of development, and it diminishes slightly in size and weight in old age. In early life it bears about the same relation to the weight of the body as in the adult.

The external coat of the spleen is the peritoneum, which is very closely adherent to the subjacent fibrous structure. The proper coat is dense and resisting, but in the human subject it is quite thin and somewhat translucent. It is composed of ordinary fibrous tissue mixed with abundant small fibres of elastic tissue and a few unstriped muscular fibres.

At the hilum the fibrous coat penetrates the substance of the spleen in the form of sheaths for the vessels and nerves. The number of the sheaths in the spleen is equal to the number of arteries that penetrate the organ. This membrane is sometimes called the capsule of Malpighi. The fibrous sheaths are closely adherent to the surrounding substance but they are united to the vessels by a loose, fibrous net-work. They follow the vessels in their ramifications to the smallest branches and are lost in the spleen-pulp. Between the sheath and the outer coat, are bands, or trabeculæ, presenting the same structure as the fibrous coat. The presence of elastic fibres in the trabeculæ can be easily demonstrated, and this kind of tissue is very abundant in the herbivora. In the carnivora the muscular tissue is particularly abundant and can be readily demonstrated; but in man this is not so easy, and the fibres are less abundant. These peculiarities in the fibrous structure are important in their relations to certain physiological changes in the size of the spleen. Its contractility may be easily demonstrated in the dog, by the application of a Faradic current to the nerves as they enter at the hilum. This is followed by a prompt and enegetic contraction of the organ. Contractions may be produced, though they are much more feeble, by applying the current directly to the spleen.

The substance of the spleen is soft and friable; and a portion of it, the spleen-pulp, may be easily pressed out with the fingers or even washed away by a stream of water. Aside from the vessels and nerves, it presents for study: 1, an arrangement of fibrous bands, or trabeculæ, by which it is divided into communicating spaces; 2, closed vesicles, called Malpighian bodies, attached to the walls of the blood-vessels; 3, a soft, reddish substance, containing large numbers of cells and free nuclei, called the spleen-pulp.

*Fibrous Structure of the Spleen* (*Trabeculæ*).—From the internal face of the investing membrane of the spleen and from the fibrous sheath of the vessels (capsule of Malpighi), are bands, or trabeculæ, which, by their interlacement, divide the substance of the organ into irregularly shaped, communicating cavities. These bands are $\frac{1}{25}$ to $\frac{1}{15}$ of an inch (1 to 1·7 mm.) broad, and are composed, like the proper coat, of ordinary fibrous tissue with elastic fibres and probably a few non-striated muscular fibres. They pass off from the capsule of Malpighi and the fibrous coat at right angles, very soon branch, interlace, and unite with each other, becoming smaller and smaller, until they measure $\frac{1}{250}$ to $\frac{1}{60}$ of an inch (0·1 to 0·42 mm.). This fibrous net-work serves as a support for the softer and more delicate parts.

*Malpighian Bodies.*—These bodies are sometimes called the splenic corpuscles or glands. They are rounded or slightly ovoid, about $\frac{1}{50}$ of an inch (0·5 mm.) in diameter, and are filled with what are thought to be lymph-corpuscles, and free nuclei. The Malpighian bodies have no investing membrane. With this difference, they resemble in structure the solitary glands of the intestine. Both the cells and the free nuclei of the splenic corpuscles bear a close resemblance to cells and nuclei found in the spleen-pulp. The corpuscles are surrounded by blood-vessels—which send branches into the interior, to form a delicate, capillary plexus—and by what is thought to be a lymphatic space or sinus.


FIG. 139.—*Malpighian corpuscle of the spleen of the cat* (Cadiat).

A, artery around which the corpuscle is placed; B, meshes of the pulp, injected; C, the artery of the corpuscle ramifying in the lymphatic tissue. The clear space around the corpuscle is the lymphatic sinus.

The number of the Malpighian corpuscles in a spleen of ordinary size has been estimated at about ten thousand (Sappey). They are readily made out in the ox and sheep but are frequently not to be discovered in the human subject. The occasional absence of these bodies constitutes another point of resemblance to the solitary glands of the small intestine.

The Malpighian bodies are attached to arteries measuring $\frac{1}{80}$ to $\frac{1}{60}$ of an inch (0·32 to 0·42 mm.) or less in diameter (Sappey). They are often found in the notch formed by the branching of an artery, but they usually lie by the sides of the vessel.

*Spleen-pulp.*—The spleen-pulp is a dark, reddish, semi-fluid substance, its color varying in intensity in different specimens. It is so soft that it may be washed by a stream of water from a thin section, and it readily decomposes, becoming then nearly fluid. It is contained in the cavities bounded by the fibrous trabeculæ, and it contains itself microscopic bands of fibres arranged in the same way. It surrounds the Malpighian bodies and contains the terminal branches of the blood-vessels, nerves and lymphatics. Upon microscopical examination, it presents free nuclei and cells like those described in the Malpighian bodies; but the nuclei are here relatively much more abundant. In addition are found, red blood-corpuscles, some natural in form and size and others more or less altered, with pigmentary granules, both free and enclosed in cells.

*Blood-vessels, Nerves and Lymphatics of the Spleen.*—The quantity of blood which the spleen receives is very large in proportion to the size of the organ.

The splenic artery is the largest branch of the cœliac axis. It is a vessel of considerable length and is remarkable for its tortuous course. In an observation by Sappey, in a man between forty and fifty years of age, the vessel measured about five inches (12 centimetres), without taking account of its deflections; and a thread placed on the vessel so as to follow exactly all its windings measured a little more than eight inches (21 centimetres). The large caliber of this vessel and its tortuous course are important points in connection with the great variations in the size of the spleen under various conditions in health and disease. The artery gives off several branches to the adjacent viscera in its course, and as it passes to the hilum, it divides into three or four branches, which again divide so as to form six to ten vessels. These penetrate the substance of the spleen, with the veins, nerves and lymphatics, enveloped in fibrous sheaths. In the substance of the spleen the arteries branch rather peculiarly, giving off many small ramifications in their course, generally at right angles to the parent trunk. These are accompanied by the veins until they are reduced to $\frac{1}{80}$ or $\frac{1}{60}$ of an inch (0·32 or 0·42 mm.) in diameter. The two classes of vessels then separate, and the arteries have attached to them the corpuscles of Malpighi. It is also a noticeable fact that the arteries passing in at the hilum have no inosculations with each other in the substance of the spleen, so that the organ is divided up into six to ten vascular compartments.

The veins join the small branches of the arteries in the spleen-pulp and pass out of the spleen in the same sheath. They anastomose quite freely in their larger as well as their smaller branches. Their caliber is estimated as about twice that of the arteries (Sappey). The estimates which have put the caliber of the veins at four or five times that of the arteries are probably much exaggerated. The number of veins emerging from the spleen is equal to the number of arteries of supply.

By most anatomists two sets of lymphatic vessels have been recognized, the superficial and the deep. The superficial lymphatics are in the investing membrane of the spleen and probably are connected with the deep lymphatics. The origin of the deep vessels is somewhat obscure. Lymphatic spaces or sinuses surround the Malpighian bodies, and there is probably a perivascular canal-system, the exact origin of which is unknown. At the hilum the deep lymphatics are joined by vessels from the surface. The vessels, numbering five or six, then pass into small lymphatic glands and empty into the thoracic duct opposite the eleventh or twelfth dorsal vertebra. No lymphatic vessels have been observed going to the spleen.

The nerves of the spleen are derived from the solar plexus. They follow the vessels in their distribution and are enclosed with them in the capsule of Malpighi. They are distributed ultimately in the spleen-pulp, but nothing definite is known of their mode of termination. When these nerves are stimulated, the non-striated muscles in the substance of the spleen are thrown into contraction.

*Some Points in the Chemical Constitution of the Spleen.*—Very little has been learned with regard to the probable uses of the spleen from analyses of its substance; and it would therefore be out of place to discuss its chemical constitution very fully. Cholesterine has been found to exist in the spleen constantly and in considerable quantity, and the same may be said of uric acid. In addition, chemists have extracted from the substance of the spleen, hypoxanthine, leucine, tyrosine, a peculiar crystallizable substance called, by Scherer, lienine, crystals of hæmatoidine, lactic acid, acetic acid, butyric acid, inosite, amyloid matter and some indefinite fatty matters.

*Variations in the Volume of the Spleen.*—One of the theories with regard to the uses of the spleen, which merits some consideration, is that it serves as a diverticulum for the blood when there is a tendency to congestion of the other abdominal viscera.

It has been shown that the spleen is greatly enlarged in dogs four or five hours after feeding, that its enlargement is at its maximum at about the fifth hour, and that it gradually diminishes to its original size during the succeeding twelve hours; but it is not apparent how far these changes are important or essential to normal digestion and absorption. Experiments have shown that animals may live, digest, and absorb alimentary matters after the spleen has been removed, and this has been observed even in the human subject. In view of these facts, it can not be assumed that the office of the spleen, as a diverticulum for the blood, is essential to the proper action of the other abdominal organs.

Changes in the volume of the spleen may be produced by operating on the nervous system, chiefly through the vaso-motor nerves. Section of the nerves at the hilum increases the size of the spleen by increasing the quantity of blood which it receives; and stimulation of these nerves produces contraction of the spleen. It is stated that stimulation of the medulla oblongata diminishes the size of the spleen, and that the same result can be produced by reflex action, stimulating the central ends of the pneumogastrics or of various sensory nerves, provided that the splanchnic nerves be intact. Starting from the medulla oblongata, the nerve-fibres which influence the size of the spleen pass down the spinal cord to the lower dorsal region, enter the semilunar ganglion by the left splanchnic, and are distributed to the spleen through the splenic plexus.

*Extirpation of the Spleen.*—There is one experimental fact that has presented itself in opposition to nearly every theory advanced with regard to the uses of the spleen, which is that the organ may be removed from a living animal and yet all the processes of life go on apparently as before. The spleen is certainly not necessary to life, nor, as far as is known, is it essential to any of the important general functions. It has been removed from dogs, cats, and even from the human subject, and its absence is attended with no constant and definite changes in the phenomena of life. If it act as a diverticulum, this is not essential to normal digestion and absorption; and if its office be the destruction or the formation of the blood-corpuscles, the formation of leucocytes, of uric acid, cholesterine or of any excrementitious matter, there are other organs which may perform these acts. Extirpation of the spleen is an old and a very common experiment. In the works of Malpighi, published in 1687, is an account of an experiment on a dog, in which the spleen was destroyed and the operation was followed by no serious results. Since then it has been removed so often, and the experiments have been so universally negative in their results, that it is hardly necessary to cite authorities upon the subject. There are many instances, also, in which it has been in part or entirely removed from the human subject, which it is unnecessary to refer to in detail. One of the phenomena following extirpation of the spleen is a modification of the appetite. Great voracity in animals after removal of the spleen was noted by the earlier observers. Later experimenters have observed this change in the appetite and have noted that digestion and assimilation do not appear to be disturbed, the animals becoming unusually fat. Dalton has also observed that the animals, particularly dogs, sometimes present a remarkable change in their disposition, becoming unnaturally ferocious and aggressive.

In the following observation these phenomena were very well marked:

The spleen was removed from a young dog weighing twenty-two pounds (about 10 kilos.). Before the operation the dog presented nothing unusual, either in his appetite or disposition. The wound healed rapidly, and after recovery had taken place, the animal was fed moderately once a day. It was noticed, however, that the appetite was voracious. The dog became so irritable and ferocious that it was dangerous to approach him, and it became necessary to separate him from the other animals in the laboratory. He would eat refuse from the dissecting-room, the flesh of dogs, fæces etc. About six weeks after the operation, having been well fed twenty-four hours before, the dog ate at one time a little more than four pounds (1,814 grammes) of beef-heart, nearly one-fifth of his weight. This he digested well, and the appetite was undiminished on the following day. This dog had a remarkably sleek and well nourished appearance (Flint, 1861).

The above is a striking example of the change in the appetite and disposition of animals after extirpation of the spleen; but these results are by no means invariable. In many instances of removal of the spleen from dogs, the animals were kept for several months and nothing unusual was observed. On the other hand, the change in disposition and the development of an unnatural appetite were observed in animals after removal of one kidney. These effects were also very well marked in an animal with biliary fistula, that lived for thirty-eight days. In the latter instance, the voracity could be accounted for by the disturbance in digestion and assimilation produced by shutting off the bile from the intestine; but these phenomena occurring after removal of one kidney are not so readily explained.

Cases are on record of congenital absence of the spleen in the human subject, in which no special phenomena had been observed during life.

Aside from certain uses which are connected with changes in its volume, it is certain that the spleen has some relation to the formation of the blood-corpuscles, both white and red. In certain cases of leucocythæmia, the spleen is in a condition of hyperplastic enlargement. The blood coming from the spleen is peculiarly rich in leucocytes, but the proportion of its red corpuscles is diminished. It may be that the spleen destroys a certain number of red corpuscles, the coloring matter being changed into other pigmentary matters, and that it also produces new red corpuscles. After removal of the spleen, the red blood-corpuscles are diminished in number, and the proportion of leucocytes is increased. This condition continues for about six months, but after that time, in dogs, the marrow of the long bones, which normally is yellow, becomes red, assuming the character of the marrow concerned in the formation of red corpuscles. Temporary diminution of red corpuscles and increase of leucocytes have been observed in the blood in cases of extirpation of the spleen in the human subject.

Whatever uses the spleen has in connection with the development of red and of white blood-corpuscles it shares with the red marrow of the bones and the so-called lymphatic glands.

The above expresses about all that is known with regard to the physiology of the spleen.

## Suprarenal Capsules.

The suprarenal capsules, as their name implies, are situated above the kidneys. They are small, triangular, flattened bodies, situated behind the peritoneum and capping the kidneys at the anterior portion of their superior ends. The left capsule is a little larger than the right and is rather semilunar in form, the right being more nearly triangular. Their size and weight are very variable in different individuals. It may be stated, as an average, that each capsule weighs about one hundred grains (6·5 grammes). The capsules are about an inch and a half (38 mm.) in length, a little less in width, and a little less than one-fourth of an inch (6·4 mm.) in thickness.

The weight of the capsules, in proportion to the weight of the kidneys, presents great variations at different periods of life. They are relatively much larger in the fœtus than after birth. They are easily distinguished in the fœtus of two months; at the end of the third month they are a little larger and heavier than the kidneys; they are equal in size to the kidneys—though a little lighter—at four months; and at the beginning of the sixth month they are to the kidneys as two to five (Meckel). In the fœtus at term the proportion is as one to three, and in the adult, as one to twenty-three.

The color of the capsules is whitish-yellow. They are completely covered by a thin, fibrous coat, which penetrates their interior, in the form of trabeculæ. Upon section they present a cortical and a medullary substance. The cortex is yellowish and $\frac{1}{25}$ to $\frac{1}{12}$ of an inch (1 to 2 mm.) in thickness. It surrounds the capsule completely and constitutes about two-thirds of its substance. The medullary substance is whitish, very vascular, and is remarkably prone to decomposition, so that it is desirable to study the anatomy of these bodies in specimens that are perfectly fresh.

*Cortical Substance.*—The cortical substance is divided into two layers. The external layer is pale-yellow and is composed of closed vesicles, rounded or ovoid in form, containing an albuminoid fluid, cells, nuclei and fatty globules. This layer is very thin. The greater part of the cortical substance is of a reddish-brown color and is composed either of closed tubes containing cells or of columns of cells surrounded by delicate, fibrous trabeculæ. On making thin sections through the cortical substance previously hardened in chromic acid and rendered clear by glycerine, rows of cells are seen, arranged with great regularity, and extending, apparently, from the investing membrane to the medullary substance. The cells appear to be enclosed in tubes measuring $\frac{1}{1000}$ to $\frac{1}{300}$ of an inch (25 to 80 $\mu$) in diameter. They are granular, with a distinct nucleus and nucleolus and a variable number of oil-globules. They measure $\frac{1}{1750}$ to $\frac{1}{1000}$ of an inch (14 to 25 $\mu$) in diameter. Between the rows of cells of the cortical substance, are bands of fibrous tissue connected with the investing membrane of the capsule.

*Medullary Substance.*—The medullary substance is much paler and more transparent than the cortex. In its centre are openings which mark the passage of its venous sinuses. It is penetrated in every direction by very delicate bands of fibrous tissue, which enclose blood-vessels, nerves, and elongated, closed vesicles containing cells, nuclei and granular matter. These vesicles, which are $\frac{1}{80}$ of an inch (0·32 mm.) long and about $\frac{1}{400}$ of an inch (64 $\mu$) broad, have been demonstrated in the ox and in the human subject. The cells in the human subject are $\frac{1}{1700}$ to $\frac{1}{1200}$ of an inch (15 to 20 $\mu$) in diameter. They are isolated with difficulty and are very irregular in their form. The nuclei measure about $\frac{1}{2500}$ of an inch (10 $\mu$). The medullary substance is peculiarly rich in vessels and nerves.


FIG. 140.—*Section of a human suprarenal capsule* (Cadiat).
A, fibrous coat; B, cells of the cortical substance, arranged in rows; C, vesicles of the medullary substance; D, blood-vessels.

*Vessels and Nerves.*—The blood-vessels going to the suprarenal capsules are very abundant and are derived from the aorta, the phrenic artery, the cœliac axis and the renal artery. Sometimes as many as twenty distinct vessels penetrate each capsule. In the cortical substance the capillaries are arranged in elongated meshes, anastomosing freely and surrounding the tubes but never penetrating them. In the medullary substance the meshes are more rounded, and here the vessels form a very rich capillary plexus. Two large veins pass out, to empty, on the right side, into the vena cava, and on the left, into the renal vein. Other smaller veins empty into the vena cava, the renal and the phrenic veins.

The nerves are very abundant and are derived from the semilunar ganglia, the renal plexus, the pneumogastric and the phrenic. Kölliker counted in the human subject thirty-three nervous trunks entering the right suprarenal capsule. The nerves probably pass directly to the medullary substance, but here their mode of distribution is unknown. In the medullary substance, however, there are two ganglia situated close to the central vein.

Nothing is known of lymphatics in the suprarenal capsules, and the existence of such vessels is doubtful.

*Chemical Reactions of the Suprarenal Capsules.*—Vulpian has described (1856), in the medullary portion of the suprarenal capsules, a peculiar substance, soluble in water and in alcohol, which gave a greenish reaction with the salts of iron and a peculiar rose-tint on the addition of iodine. He could not determine the same reaction with extracts from any other parts. Later, in conjunction with Cloez, he discovered hippuric and taurocholic acid in the capsules of some of the herbivora. These bodies contain in addition, leucine, hypoxanthine, taurine, fats and inorganic salts, the latter chiefly phosphates and salts of potassium.

The suprarenal capsules are not essential to life. If care be taken to avoid injury of the semilunar ganglia, they may be removed from animals and the operation apparently has no remote effects. In Addison's disease, a disorder attended with bronzing of the skin and serious and finally fatal disorder of nutrition, there usually is disorganization of the suprarenal capsules, but this is not invariable. It is not established that disorganization of the capsules stands in a causative relation to the discoloration of the skin or to the constitutional disturbance. Investigations into these diseased conditions have developed little or nothing of importance concerning the physiology of the suprarenal capsules.

## Thyroid Gland.

The thyroid gland is attached to the lower part of the larynx and follows it in its movements. Its color is brownish-red. The anterior face is convex and is covered by certain of the muscles of the neck. The posterior surface is concave and is applied to the larynx and trachea. It presents two lateral lobes, each with a rounded, thickened base below, and a long, pointed extremity extending upward, the lobes being connected by an isthmus (see Fig. 141, page 424). Each of these lobes is about two inches (50 mm.) in length, three-quarters of an inch (19 mm.) in breadth, and about the same in thickness at its thickest portion. The isthmus connects the lower portion of the lateral lobes, covers the second and third tracheal rings, and is about half an inch (12 mm.) wide and one-third of an inch (8·5 mm.) thick. From the left side of the isthmus, and sometimes from the left lobe, is a portion projecting upward, called the pyramid. The weight of the thyroid gland, according to Sappey, is three hundred and fifty to three hundred and eighty grains (22 to 24 grammes). It is usually stated by anatomical writers that it is relatively larger in the fœtus and in early life than in the adult; but according to Sappey, its weight, in proportion to the weight of the adjacent organs, does not vary with age. It is a little larger and more prominent in the female than in the male.

*Structure of the Thyroid Gland.*—The thyroid gland is covered with a thin but resisting coat of ordinary fibrous tissue, which is loosely connected with the surrounding parts. From the internal surface of this membrane, are fibrous bands, or trabeculæ, giving off, as they pass through the gland, secondary trabeculæ, and then subdividing until they become of microscopic size. By this arrangement the gland is divided up into small, communicating cells. The trabeculæ contain many small, elastic fibres. Throughout the substance of the gland, lodged in the meshes of the trabeculæ, are rounded or ovoid, closed vesicles, measuring $\frac{1}{600}$ to $\frac{1}{250}$ of an inch (40 to 100 $\mu$). These are formed of a structureless membrane and are lined by a single layer of pale, granular, nucleated cells, $\frac{1}{3000}$ to $\frac{1}{2000}$ of an inch (8 to 12 $\mu$) in diameter. The layer of cells sometimes lines the vesicle completely, sometimes it is incomplete, and sometimes it is wanting. The contents of the vesicles are a clear, yellowish, slightly viscid, albuminoid fluid, with a few granules, pale cells, and nuclei. The vesicles are arranged in the form of lobules, and between them are the great veins.

*Vessels and Nerves.*—The blood-vessels of the thyroid gland are very abundant, this organ being supplied by the superior and inferior thyroid arteries and sometimes by a branch from the innominata. The arteries break up into a close, capillary plexus, surrounding the vesicles with a rich net-work, but never penetrating their interior. The veins are large, and like the hepatic veins, they are so closely adherent to the surrounding tissue that they do not collapse when cut across. The veins emerging from the gland form a plexus over its surface and the surface of the trachea, and they then go to form the superior, middle and inferior thyroid veins. The nerves are derived from the pneumogastrics and from the cervical sympathetic ganglia. The lymphatics are abundant but are difficult to inject. The exact distribution of the nerves and the origin of the lymphatics are not well understood.

What little is known with regard to the chemical constitution of the thyroid gland is embodied in the statement that it contains leucine, xanthine, lactic acid, succinic acid and some volatile fatty acids. The blood of the thyroid veins has been analyzed, but the changes in its composition in passing through the gland are slight and indefinite. It has been asserted that one of the uses of the thyroid gland is to regulate the blood-circulation in the brain, but the observations in support of this view are not very satisfactory.

*Myxœdema.*—Important facts have lately been developed showing a connection between the thyroid gland and a disease characterized by infiltration of the connective tissues with a gelatinous substance containing mucine. This disease has been described by Ord, under the name of myxœdema. It is attended with marked impairment of the mental faculties, and a condition like cretinism. This is usually associated with disease of the thyroid gland.

Complete excision of the thyroid gland in the human subject has been followed by the peculiar mental condition characteristic of cretinism. In the lower animals the operation of complete extirpation is fatal. The experiments of Horsley, upon dogs and monkeys, show great differences in the results, depending upon age. In young animals death usually occurs in a few days, while old animals survive the operation four, five, or six months.

As far as could be ascertained from these experiments upon the lower animals—dogs and monkeys—the conditions, including the mental phenomena, resembled those observed in cases of myxœdema in the human subject, The animals operated upon were found to be exceedingly sensitive to cold. If put in a hot-air bath at a temperature of 105° Fahr. (40·5° C.) after the general symptoms made their appearance, the animals could be kept alive for several months. Horsley described the symptoms in monkeys, after three to seven weeks, as "commencing hebetude and mucinoid degeneration of the connective tissues," and after five to eight weeks, "complete imbecility and atrophy of all tissues, especially muscles."

It is difficult to draw, from these observations, absolutely definite conclusions with regard to the physiological relations of the thyroid gland. This organ seems essential to life, and its removal profoundly affects the general processes of nutrition. It influences the quantity of mucine in the body, but precisely in what way, it is difficult to determine.

## Thymus Gland.

In its anatomy the thymus resembles the ductless glands, but its office, whatever this may be, is confined to early life. In the adult the organ is wanting, traces, only, of fibrous tissue with a little fat existing after puberty in the situation previously occupied by this gland. As there never has been a plausible theory, even, of the uses of this organ, the existence of which is confined to the first two or three years of life, it seems necessary only to give a brief sketch of its structure.

The thymus appears at about the third month of fœtal life and gradually increases in size until about the end of the second year. It then undergoes atrophy and it disappears almost entirely at the age of puberty. It is situated partly in the thorax and partly in the neck. The thoracic portion is in the anterior mediastinum, resting upon the pericardium, extending as low as the fourth costal cartilage. The cervical portion extends upward as far as the lower border of the thyroid gland. The whole gland is about two inches (50·8 mm.) in length, an inch and a half (38 mm.) broad at its lower portion, and about one-quarter of an inch (6·4 mm.) thick. Its color is grayish with a slightly rosy tint. It is usually in the form of two lateral lobes lying in apposition in the median line, although sometimes there exists but a single lobe. It is composed of a number of lobules held together by connective tissue

The proper coat of the thymus is a delicate, fibrous membrane sending processes into the interior of the organ. Its fibrous structure, however, is loose, so that the lobules can be separated with little difficulty. Portions of the gland may be, as it were, unravelled, by loosening the interstitial fibrous tissue. In this way it is found to be composed of little lobular masses attached to a continuous cord. This arrangement is more distinct in the inferior animals of large size than in man. The lobules are composed of rounded vesicles, ten to fifteen in number, and $\frac{1}{125}$ to $\frac{1}{40}$ of an inch (200 to 600 $\mu$) in diameter. The walls of these vesicles are thin, finely granular and very fragile. The vesicles contain a small quantity of an albuminoid fluid, with cells and free nuclei. The cells are small and transparent, and

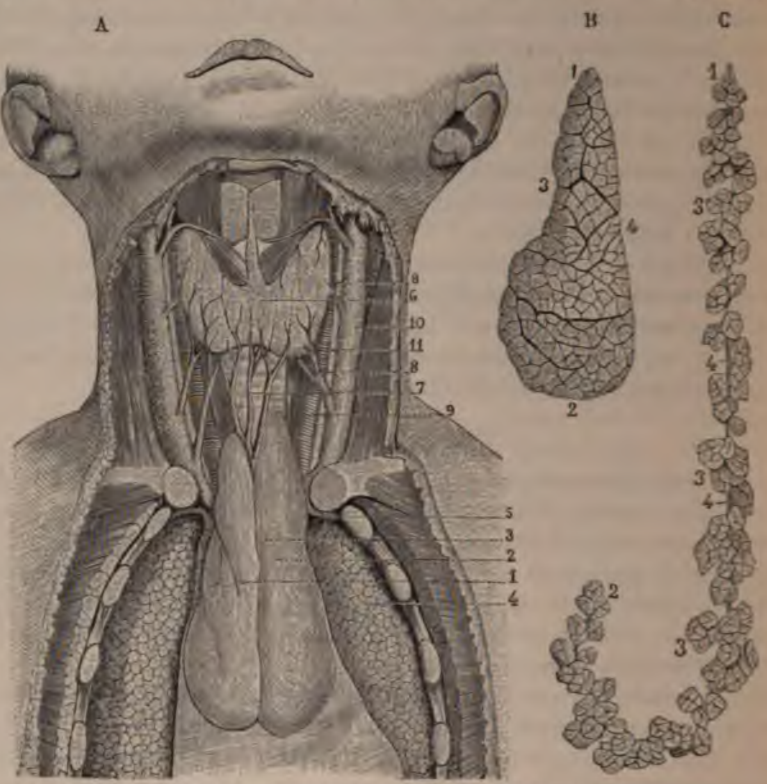


FIG. 141.—*Thyroid and thymus glands* (Sappey).

A. 1, right lobe of the thymus; 2, left lobe; 3, groove between the two lobes; 4, lungs, the anterior borders raised to show the thymus; 5, terminal branch of the internal mammary vein; 6, thyroid gland; 7, median inferior thyroid veins; 8, lateral inferior thyroid veins; 9, common carotid artery; 10, internal jugular vein; 11, pneumogastric nerve.
B. Right lobe of the thymus with the investing membrane removed. 1, upper extremity of the lobe; 2, lower extremity; 3, external border; 4, internal border.
C. Arrangement of the lobules of the same lobe, around the central cord. 1, upper extremity of the lobe; 2, lower extremity; 3, 3, 3, lobules; 4, 4, central cord.

the nuclei are spherical, relatively large, and contain one to three nucleoli. The free nuclei are also rounded and contain several distinct nucleoli. These vesicles are easily ruptured, when their contents exude in the form of an opalescent fluid, which is sometimes called the thymic juice.

Anatomists are somewhat divided in their opinions with regard to the structure of the central cord and the lobules. Some adopt the view advanced by Astley Cooper, that the cord has a central canal connected with cavities in the lobules; while others believe that the cavities thus described are produced artificially by the processes employed in anatomical investigation. The latter opinion is probably correct.

The blood-vessels of the thymus are abundant, but their caliber is small and the gland is not very vascular. They are derived chiefly from the internal mammary artery, a few coming from the inferior thyroid, with occasional branches from the superior diaphragmatic or the pericardial. They pass between the lobules, surround and penetrate the vesicles and form a capillary plexus in their interior. The vesicles in this respect bear a certain resemblance to the closed follicles of the intestine. The veins are also abundant but they do not follow the course of the arteries. The principal vein emerges at about the centre of the gland posteriorly and empties into the left brachio-cephalic. Other small veins empty into the internal mammary, the superior diaphragmatic and the pericardial. A few nervous filaments from the sympathetic surround the principal thymic artery and penetrate the gland. Their ultimate distribution is uncertain. The lymphatics are very abundant.

As regards its chemical constitution, it may be stated in general terms that the thymus contains matters of about the same character as those found in the other ductless glands.

Inasmuch as the thymus is peculiar to early life, one of the most important points in its anatomical history relates to its mode of development. This, however, does not present any great physiological interest and is fully treated of in works upon anatomy.

## Pituitary Body and Pineal Gland.

These little bodies, situated at the base of the brain, are quite vascular, contain closed vesicles and but few nervous elements, and are sometimes classed with the ductless glands. Physiologists have no definite idea of their uses.

The pituitary body is of an ovoid form, a reddish-gray color, weighs five to ten grains (0·324 to 0·648 grammes), and is situated on the sella Turcica of the sphenoid bone. It is said to be larger in the fœtus than in the adult, and in fœtal life it has a cavity communicating with the third ventricle. This little body has been studied by Grandry, in connection with the suprarenal capsules. He regarded it as essentially composed of closed vesicles, with fibres of connective tissue and blood-vessels. The vesicles are formed of a transparent membrane, containing irregularly polygonal, nucleated cells and free nuclei. The nuclei are distinct, with a well marked nucleolus. Capillary vessels surround these vesicles without penetrating them. Grandry did not observe either nerve-cells or fibres between the vesicles.

The pineal gland is situated just behind the posterior commissure of the brain, between the nates, and is enclosed in the velum interpositum. It is of a conical shape, one-third of an inch (8·5 mm.) in length and of nearly the color of the pituitary body. It is connected with the base of the brain by several delicate, commissural peduncles. It presents a small cavity at its base, and frequently it contains in its substance little calcareous masses composed of calcium phosphate, calcium carbonate, ammonio-magnesian phosphate and a small quantity of organic matter. It is covered with a fibrous envelope which sends processes into its interior. As the result of the researches of Grandry, it has been found to present a cortical substance, analogous in its structure to the pituitary body, and a central portion composed of the ordinary nervous elements found in the gray matter of the brain. Its structure is very like that of the medullary portion of the suprarenal capsules (Grandry).

It is difficult to classify organs, of the uses of which physiologists are entirely ignorant; but in structure, the little bodies just described certainly resemble the ductless glands.

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## CHAPTER XIV.

### *NUTRITION—ANIMAL HEAT AND FORCE.*

Nature of the forces involved in nutrition—Life, as represented in development and nutrition—Substances which pass through the organism—Metabolism—Substances consumed in the organism—Conditions which influence nutrition—Animal heat and force—Estimated quantity of heat produced by the body—Limits of variation in the normal temperature in man—Variations with external temperature—Variations in different parts of the body—Variations at different periods of life etc.—Influence of exercise etc., upon the heat of the body—Influence of the nervous system upon the production of animal heat (heat-centres)—Mechanism of the production of animal heat—Equalization of the animal temperature—Relations of heat to force.

Nutrition proper, in the light in which it is proposed to consider it in this chapter, is the process by which the physiological wear of the tissues and fluids of the body is compensated by the appropriation of new matter. All of the physiological operations that have thus far been described, including the circulation of the blood, respiration, alimentation, digestion, absorption and secretion, are to be regarded as means directed to a single end; and the great end, to which all of the functions enumerated are subservient, is the general process of nutrition.

The nature of the main forces involved in nutrition, be it in a highly organized part, like the brain or muscles, or in a tissue called extra-vascular, like the cartilages or nails, is unknown. The phenomena attending the general process, however, have been carefully studied, and certain important positive results have been attained; but there is really no more satisfactory explanation of the nature of the causative force of nutrition to be found in the doctrines of to-day than in the speculative theories of the past.

The blood contains all the matters that enter into the composition of the tissues and secretions, either identical with them in form and composition, as is the case in most of the inorganic matters, or in a condition which admits of their transformation into the characteristic constituents of the tissues, as in the organic substances proper. These matters are supplied to the tissues, in the required quantity, through the circulatory apparatus; and oxygen, which is immediately indispensable to all the operations of life, is introduced by respiration. The great nutritive fluid, being constantly drawn upon by the tissues for materials for their regeneration, is kept at the proper standard by the introduction of new matter into the system in alimentation, its elaborate preparation by digestion, and its appropriation by the fluids by absorption. Many of these processes require the action of certain secretions.

The introduction of new matter, so essential to the continuance of the phenomena of life, is demanded, on account of the change of the substance of the tissues into what is called effete matter; and this is discharged from the animal organism, to be appropriated by vegetables and thus maintain the equilibrium between the animal and the vegetable kingdoms.

It is a well established fact that nearly all of the tissues undergo disassimilation, or conversion into effete matter, during their physiological wear in the living organism, while others, like the epidermis and its appendages, are gradually desquamated, and when once formed, do not pass through any farther changes. The whole question of the essence and nature of the nutritive property or force resolves itself into vitality. Life is always attended with what are known as the phenomena of nutrition, and nutrition does not exist except in living organisms. At present, physiologists have been able to define life only by a recital of certain of its invariable and characteristic attendant conditions; and yet there are few if any definitions of life—regarding life as the sum of the phenomena peculiar to living organisms—that are not open to grave objections.

If life be regarded as a principle, it stands in the relation of a cause to the vital phenomena; if it be regarded as the totality of these phenomena, it is an effect.

In the study of the development of a fecundated ovum, life seems to be a principle, giving the property of appropriating matter from without, until the germ becomes changed, from a globule of microscopic size and comparatively simple structure, into a complete organism with highly elaborated parts. This organism has a definite form and size, a definite period of existence, and it produces, at a certain time, generative elements, capable of perpetuating its life in new beings. It may be said that an organism dies physiologically because the vital principle, if such a principle be admitted, has a limited term of existence; but on the other hand, the fully developed living organism, called an animal, presents many distinct parts, each endowed with an independent property called vital, that property recognized by Haller in various tissues, under the name of irritability; and it is the co-ordinated association of these vitalities that constitutes the perfect being. These are more or less distinct; and a sudden and simultaneous arrest of the physiological properties in all the tissues, in what is called death, is not often observed. For example, the nerves may die before the muscles, or the muscles, before the nerves. It is found, also, that physiological properties, apparently lost or destroyed, may be made to return; as in resuscitation after asphyxia or in the restoration of muscular or nervous excitability by injection of blood.

The life of a fecundated ovum is the property which enables it to undergo development when placed under favorable conditions; and by the surrounding conditions, its development may be arrested, suspended or modified. The life of a non-fecundated ovum is like that of any ordinary anatomical element.

The life of an anatomical element or tissue in process of development is the property by virtue of which it arrives at its perfection of organization and performs certain defined offices, as far as its organization will permit. This can also be destroyed, suspended or modified by surrounding conditions.

The life of a perfected anatomical element or tissue is the property which enables it to regenerate itself and perform it offices, subject, also, to modifications from surrounding conditions.

The life of a perfect animal organism is the sum of the vitalities of its constituent parts; but a being may live with the physiological properties of certain parts abolished or seriously modified, as a man exists and preserves his identity with a limb amputated. Life may continue for a long time without consciousness or with organs paralyzed; but certain functions, such as respiration and circulation, are indispensable to the nutrition of all parts, the properties of the different tissues are speedily lost when these processes are arrested, and the being then ceases to exist.

These considerations make it evident that it is difficult if not impossible to give a single, comprehensive definition of life, a study of the varied phenomena of which constitutes the science of physiology.

The general process of nutrition begins with the introduction of matter from without, called food. It is carried on by the appropriation of this matter by the organism. It is attended with the production of excrementitious matters and the development of certain phenomena that remain to be studied, the most important of which is the production of heat.

The term metabolism, now used by many English writers, seems destined to become generally adopted. It was employed by Schwann to designate a kind of action by cells, resulting in a change in the character of substances brought in contact with them. Modern writers use it as a translation of the German word *Stoffwechsel.* The literal signification of the Greek word μεταβολή is change. As applied to nutritive changes, metabolism is equivalent to assimilation; and as applied to the changes which result in the production of effete matters, it is equivalent to disassimilation, a term much used by the French, and one which well expresses changes that are exactly the opposite of assimilation. The signification of the term metabolism seems likely to be extended so as to include the acts of cells in the production of the constituents of the secretions, a process which it is difficult to express in a single word.

The behavior of various substances in nutrition has already been treated of, to some extent, in connection with alimentation; but certain general relations of nutritive substances to assimilation remain to be considered. It is convenient, as before, to divide these substances into the following classes: 1, Inorganic; 2, organic non-nitrogenized; 3, organic nitrogenized. The excrementitious products constitute a distinct class by themselves.

### Substances which pass through the Organism.

All of the inorganic matters taken in with the food pass out of the organism, generally in the form in which they enter, in the fæces, urine and perspiration; but it must not be inferred from this fact that they are not useful as constituent parts of the body. Some of these, such as water and the chlorides, have important uses of a purely physical character. It is necessary, for example, that the blood should contain a certain proportion of sodium chloride, this substance modifying and regulating the processes of absorption and probably of assimilation. In addition, however, the chlorides exist as constituent parts of every tissue and organ of the body, and they are so closely united with the nitrogenized matters that they can not be completely separated without incineration. Those inorganic matters, the uses of which are so important in their passage through the body, are found largely as constituents of the fluids and are less abundant in the solids. They are contained in large proportion, also, in the liquid excretions; and any excess over the quantity actually required by the system is thrown off in this way. Other inorganic matters are specially important as constituent parts of the tissues, and they are more abundant in the solids than in the fluids. Examples of substances of this class are the calcium salts, particularly the phosphates. These are also in a condition of intimate union with organic matters.

If certain simple chemical changes be excepted, such as the decomposition of the bicarbonates, the inorganic constituents of food do not necessarily undergo any modification in digestion. They are generally introduced already in combination with organic matters, and they accompany them in the changes which they pass through in digestion, assimilation by the blood, deposition in the tissues, and the final transformations that result in the various excrementitious products; so that the inorganic salts are found united with the organic matter of the food as it enters the body, and what seem to be the same substances, in connection with the organic excrementitious matters. Between these two conditions, however, are the various operations of assimilation and disassimilation, or metabolism, from which inorganic matters are never absent.

*Inorganic Constituents of the Body.*—The number of inorganic substances now well established as existing in the human body is about twenty-one; but some are found in small quantities, are not always present and apparently have no very important uses. These will be passed over rapidly, as well as those which are so intimately connected with some important function as to render their full consideration in connection with that function indispensable.

*Gases.*—The gases (oxygen, hydrogen, nitrogen, carburetted hydrogen and hydrogen monosulphide) exist both in a gaseous state and in solution in some of the fluids of the body. Oxygen plays a most important part in the function of respiration; but the office of the other gases is by no means so essential. Nitrogen seems to be formed by the system in small quantity and is taken up by the blood and exhaled by the lungs, except during inanition, when the blood absorbs a little from the inspired air. It exists in greatest quantity in the intestinal canal. Carburetted hydrogen and hydrogen monosulphide, with pure hydrogen, are found in minute quantities in the expired air and exist in a gaseous state in the alimentary canal. From the offensive nature of the contents of the large intestine, one would suspect the presence of hydrogen monosulphide in considerable quantity; but actual analysis has shown that the gas contained in the stomach and in the small and large intestines is composed chiefly of nitrogen, with hydrogen and carburetted hydrogen in about equal proportions (five to eleven parts per hundred), and but a trace of hydrogen monosulphide. With the exception, then, of oxygen and carbon dioxide, the latter being an excretion, the gases do not hold an important place among the constituents of the organism. At all events, their uses, whether they be important or not, are but little understood.

*Water.*—Water exists in all parts of the body; in the fluids, some of which, as the lachrymal fluid and perspiration, contain little else, and in the hardest structures, as the bones and the enamel of the teeth. In the solids and semi-solids it does not exist as water, but it enters into their composition, assuming the consistence by which the tissues are characterized.

The quantity of water which each organic substance contains is important; and it is provided that this quantity, though indefinite, shall not exceed or fall below certain limits. All organs and tissues must contain a tolerably definite quantity of water to give them proper consistence. The effects of too great a proportion of water in the system are well known to physicians. General muscular debility, loss of appetite, dropsies and various other indications of imperfect nutrition are among the results of such a condition; while a deficiency of water is immediately made known by the sensation of thirst, which leads to its introduction from without.

The fact that water never exists in any of the fluids, semi-solids or solids, without being combined with inorganic salts, especially sodium chloride, is one reason why its proportion in various situations is nearly constant. The presence of these salts influences, in the semi-solids at least, the quantity of water entering into their composition, and consequently it regulates their consistence. The nutrient fluid of the muscles during life contains water with just enough saline matter to preserve the normal consistence of the parts. This action of saline matters is even more apparent in the case of the blood-corpuscles. If pure water be added to the blood, these bodies swell up and are finally dissolved; while on the addition of a strong solution of salt, they lose water and become shrunken and corrugated. Their natural form and consistence can be restored, however, even after they have been completely dried, by adding water containing about the proportion of salt which exists in the blood-plasma. It seems clear, then, that water is a a necessary part of all tissues and is especially important to the proper constitution of organic nitrogenized substances; that it enters into the constitution of these substances, not as pure water, but always in connection with certain inorganic salts; that its proportion is confined within certain limits; and that the quantity in which it exists, in organic nitrogenized substances particularly, is regulated by the quantity of salts which enter, with it, into the constitution of these substances.

The quantities of water which can be driven off by a moderate temperature (212° Fahr., or 100° C.), from the different fluids and tissues of the body, vary of course very considerably according to the consistence of the parts. The following is a list of the quantities in the most important fluids and solids (Robin and Verdeil):

TABLE OF QUANTITIES OF WATER.

| | | Parts per 1,000. |
|---|---|---|
| Solids and semi-solids. | In the enamel of the teeth | 2 |
| | In epithelial desquamation | 37 |
| | In teeth | 100 |
| | In bones | 130 |
| | In tendons (Burdach) | 500 |
| | In articular cartilages | 550 |
| | In skin (Weinholt) | 575 |
| | In liver (Frommherz and Gugert) | 618 |
| | In muscles of man (Bibra) | 725 |
| | In ligaments (Chevreul) | 768 |
| Liquids. | In the blood of man (Becquerel and Rodier) | 780 |
| | In milk of the human female (Simon) | 887 |
| | In chyle of man (Rees) | 904 |
| | In bile | 905 |
| | In urine | 933 |
| | In human lymph (Tiedemann and Gmelin) | 960 |
| | In human saliva (Mitscherlich) | 983 |
| | In gastric juice | 984 |
| | In perspiration | 986 |
| | In tears | 990 |

*Uses of Water.*—After what has been stated with regard to the condition in which water exists in the body, there remains but little to say concerning its uses. As a constituent of organized tissues, it gives to cartilage its elasticity, and to tendons their pliability and toughness; it is necessary to the power of resistance of the bones, and it is essential to the proper consistence of all parts of the body. It also has other important uses, as a solvent. Soluble articles of food are introduced in solution in water. The excrementitious products, which generally are soluble in water, are dissolved by it in the blood, are carried to the organs of excretion, and are discharged in a watery solution from the body.

*Origin and Discharge of Water.*—It is evident that a great proportion of the water in the organism is introduced from without, in the fluids and in the watery constituents of all kinds of food; but water is also formed in the body by a direct union of oxygen and hydrogen. The evidences of formation of water in the body have already been given, in connection with the question of water considered as a product of excretion, and will be again discussed in treating of the relations of water to the processes of calorification. In the discharge of water by the kidneys and skin, it has long been observed that in point of activity these two emunctories bear a certain relation to each other. When the skin is inactive, as in cold weather, the kidneys discharge a large quantity of water; and when the skin is active, the quantity of water discharged by the kidneys is proportionally diminished.

*Sodium Chloride.*—Sodium chloride is next in importance, as an inorganic constituent of the organism, to water. It is found in the body at all periods of life, existing even in the ovum. It exists in all the fluids and solids of the body, with the single exception of the enamel of the teeth. The exact quantity in the entire body has never been ascertained; nor, indeed, has any accurate estimate been made of the quantity contained in the various tissues, for all the chlorides are generally estimated together. It exists in greatest proportion in the fluids, giving to some of them, as the tears and perspiration, a distinctly saline taste. The following table gives the quantities found in some of the most important of the fluids and solids:

TABLE OF QUANTITIES OF CHLORIDES.

| | Parts per 1,000. |
|---|---|
| In blood, human (Lehmann) | 4·210 |
| In chyle (Lehmann) | 5·310 |
| In lymph (Nasse) | 4·120 |
| In milk, human (Lehmann) | 0·870 |
| In saliva, human (Lehmann) | 1·530 |
| In perspiration, human (mean of three analyses, Piutti) | 3·433 |
| In urine (maximum) Valentin. | 7·280 |
| In urine (mean) Valentin. | 4·610 |
| In urine (minimum) Valentin. | 2·400 |
| In fæcal matters (Berzelius) | 3·010 |

*Uses of Sodium Chloride.*—The uses of sodium chloride are undoubtedly important, but are not yet fully understood. While it enters into the composition of the organized solids and semi-solids, as an important and essential constituent, it seems to exercise its chief office in the liquids. It is the sodium chloride particularly which regulates the quantity of water entering into the composition of the blood-corpuscles, thereby preserving their form and consistence; and it seems to perform an analogous office with regard to the other semi-solids of the body. The following brief statement expresses the general uses of this substance in the economy:

"Common salt is intermediate in certain general processes and does not participate by its elements in the formation of organs" (Liebig).

In the first place, the fluids of the body are generally intermediate in their uses, containing nutritious matters, which are destined to be appropriated by the tissues and organs, and excrementitious matters, which are to be separated from the body. In the blood and chyle, sodium chloride is found in greatest abundance. In the nutrition of tissues and organs, sodium chloride is not deposited in any considerable quantity, but it seems to regulate the general process, at least to a certain extent. In all civilized countries salt is used extensively as a condiment, and it undoubtedly facilitates digestion by rendering the food more savory and increasing the flow of the digestive fluids; here, likewise, acting simply as an intermediate agent. There is nothing more general among men and animals than this desire for common salt. In the experiments made by Dailly on sheep and by Boussingault on bullocks, depriving these animals as nearly as possible of common salt for a number of months, the general nutrition was affected without any marked change in special tissues or organs.

It is significant that the quantity of sodium chloride existing in the blood is not subject to variation, but that an excess introduced with the food is thrown off by the kidneys. The quantity in the urine, then, bears a relation to the quantity introduced with food, but the proportion in the blood is nearly constant. This is another fact in favor of the view that the presence of a definite quantity of common salt in the circulating fluid is essential to normal nutrition.

*Origin and Discharge of Sodium Chloride.*—Sodium chloride is always introduced with food, in the condition in which it is found in the body. It is contained in the substance of all kinds of food, animal and vegetable; but in the herbivora and in man, this source is not sufficient to supply the wants of the system, and it is introduced, therefore, as salt. The quantity which is discharged from the body has been estimated by Barral to be somewhat less than the quantity introduced, about one-fifth disappearing; but these estimates are not entirely accurate, for the quantity thrown off in the perspiration has never been directly ascertained. It exists in the blood in connection with potassium phosphate, and a certain quantity is lost in a double decomposition which takes place between these two salts, resulting in the formation of potassium chloride and sodium phosphate. It also is supposed to furnish sodium to all the salts which have a sodium base, and a certain quantity, therefore, disappears in this way.

Existing, as it does, in all the solids and fluids of the body, sodium chloride is discharged in all the excretions, being thrown off in the urine, fæces, perspiration and mucus.

*Potassium Chloride.*—Potassium chloride, although neither so important as sodium chloride nor so generally distributed in the economy, seems to have analogous uses. It is found in the muscles, liver, milk, chyle, blood, mucus, saliva, bile, gastric juice, cephalo-rachidian fluid and urine. It is very soluble, and in these situations it exists in solution in the fluids. Its quantity in the fluids has not been accurately ascertained, as it has generally been estimated in connection with sodium chloride. In the muscles it exists, however, in a larger proportion than common salt. In cow's milk, Berzelius found 1·7 part per 1,000. Pfaff and Schwartz found 1·35 per 1,000 in cow's milk and 0·3 per 1,000 in human milk. Of the uses of this salt, little remains to be said after what has been stated with regard to sodium chloride. The uses of these two salts are probably identical, although sodium chloride, on account of its greater quantity in the fluids and its universal distribution, is by far the more important.

*Origin and Discharge of Potassium Chloride.*—This substance has two sources; one in the food, existing, as it does, in muscular tissue, milk etc., and the other in a chemical reaction between potassium phosphate and sodium chloride, forming potassium chloride and sodium phosphate. That this decomposition takes place in the body, is evident from the fact that the ingestion of a considerable quantity of common salt has been found, in the sheep, to increase the quantity of potassium chloride in the urine, without having any influence upon the quantity of sodium chloride. Potassium chloride is discharged from the body in the urine and in mucus.

*Calcium Phosphate.*—This salt is found in all the solids and fluids of the body. As it is always united, in the solids, with organic substances as an important element of constitution, it is hardly second in importance to water.

It differs in its uses so essentially from the chlorides, that they are hardly to be compared. It is insoluble in water, but is held in solution in the fluids of the body by virtue of free carbon dioxide, the bicarbonates and sodium chloride. In the solids and semi-solids, the condition of its existence is the same as that of water; *i. e.* it is incorporated with the organic substance characteristic of the tissue, is one of its essential constituents, and can not be completely separated without incineration. Nothing need be added here with regard to this mode of union in the body, of organic and inorganic substances, after what has been said with regard to water.

The following table gives the relative quantities of calcium phosphate in various situations:

TABLE OF QUANTITIES OF CALCIUM PHOSPHATE.

| | | Parts per 1,000 |
|---|---|---|
| In arterial blood. | Poggiale and Marchal. | 0·79 |
| In venous blood. | Poggiale and Marchal. | 0·76 |
| In milk, human (Pfaff and Schwartz) | | 2·50 |
| In saliva (Wright) | | 0·60 |
| In urine, proportion to weight of ash (Fleitmann) | | 25·70 |
| In excrements (Berzelius) | | 40·00 |
| In bone (Lassaigne) | | 400·00 |
| In the vertebræ of a rachitic patient (Bostock) | | 136·00 |
| In teeth of an infant one day old | Lassaigne. | 510·00 |
| In teeth of the adult | Lassaigne. | 610·00 |
| In teeth, at eighty-one years | Lassaigne. | 660·00 |
| In the enamel of the teeth | Lassaigne. | 885·00 |

By this table it is seen that calcium phosphate exists in very small quantity in the fluids but is abundant in the solids. In the latter, the quantity is in proportion to the hardness of the structure, the quantity in enamel, for example, being more than twice that in bone. The variations in quantity with age are very considerable. In the teeth of an infant one day old, Lassaigne found 510 parts per 1,000; in the teeth of an adult, 610 parts; and in the teeth of an old man of eighty-one years, 660 parts. This increase in the calcareous constituents of the bones, teeth etc., in old age is very marked; and in extreme old age they are deposited in considerable quantity in situations where there existed but a small proportion in adult life. The system seems to gradually lose the property of appropriating to itself organic matters; and although articles of food may be digested as well as ever, the power of assimilation by the tissues is diminished. The bones become brittle, and fractures, therefore, are common at this period of life, when dislocations are almost unknown. Inasmuch as the efficiency of organs depends mainly upon organic matters, the system actually wears out, and this progressive change finally unfits certain parts for their various offices. An individual, if he escape accidents and die of old age, passes away by a simple wearing out of some essential part or parts of the organism.

*Uses of Calcium Phosphate.*—This substance, as before remarked, enters largely into the constitution of the solids of the body. In the bones its office is most apparent. Its existence, in suitable proportion, is necessary to the mechanical uses of these parts, giving them their power of resistance without rendering them too brittle. It is more abundant in the bones of the lower extremities, which have to sustain the weight of the body, than in the upper extremities; and in the ribs, which are elastic rather than resisting, it exists in less quantity than in the bones of the arm.

The necessity of a proper proportion of calcium phosphate in the bones is made evident by cases of disease. In rachitis, where, as is seen by the table, its quantity is very much diminished, the bones being unable to sustain the weight of the body become deformed; and finally, when calcium phosphate is deposited, they retain their distorted shape.

*Origin and Discharge of Calcium Phosphate.*—The origin of calcium phosphate is exclusively from the external world. It enters into the constitution of food and is discharged in the fæces, urine and other matters thrown off by the body. Its proportion in the urine is very variable.

*Calcium Carbonate.*—This salt exists in the bones, teeth, cartilage, internal ear, blood, sebaceous matter and sometimes in the urine. It exists as a normal constituent of the urine in some herbivora but not in the carnivora or in man. It is most appropriately considered immediately after calcium phosphate, because it is the salt next in importance in the constitution of the bones and teeth. In these structures it exists intimately combined with the organic matter, under the same conditions as the phosphates, and it has analogous uses. In the fluids it exists in small quantity and is held in solution by virtue of free carbon dioxide and potassium chloride.

Calcium carbonate is the only example of an inorganic salt existing uncombined and in a crystalline form in the body. In the internal ear it is found in this form and has some office connected with audition.

TABLE OF QUANTITIES OF CALCIUM CARBONATE.

| | | Parts per 1,000. |
|---|---|---|
| In bone, human (Berzelius) | | 113·00 |
| " " " (Marchand) | | 102·00 |
| " " " (Lassaigne) | | 76·00 |
| In teeth of an infant one day old | Lassaigne. | 140·00 |
| In teeth of an adult | Lassaigne. | 100·00 |
| In teeth of an old man, eighty-one years | Lassaigne. | 10·00 |
| In urine of the horse (Boussingault) | | 10·82 |

*Origin and Discharge of Calcium Carbonate.*—This salt is introduced into the body with food, held in solution in water by the carbon dioxide, which is always present in small quantity. It is also formed in the body, particularly in the herbivora, by a decomposition of the calcium tartrates, malates, citrates and acetates contained in the food. These salts, meeting with carbon dioxide, are decomposed and calcium carbonate is formed. It is probable that in the human subject some of it is changed into calcium phosphate and in this form is discharged in the urine; but it has not been definitely ascertained when and how this change takes place.

*Sodium Carbonate.*—This salt is found in the blood and saliva, giving to these fluids their alkalinity; in the urine of the human subject when it is alkaline without being ammoniacal; in the urine of the herbivora; and in the lymph, cephalo-rachidian fluid and bone. The analyses by different chemists, with regard to this substance, are very contradictory, on account of its formation during the process of incineration; but there is no doubt that it is found in the above situations. The following table gives the quantities which have been found in some of the fluids and solids:

TABLE OF QUANTITIES OF SODIUM CARBONATE.

| | Parts per 1,000. |
|---|---|
| In blood of the ox (Marcet) | 1·62 |
| In lymph (Nasse) | 0·56 |
| In cephalo-rachidian fluid (Lassaigne) | 0·60 |
| In compact tissue of the tibia in a male of 38 years (Valentin) | 2·00 |
| In spongy tissue of the same (Valentin) | 0·70 |

*Uses of Sodium Carbonate.*—This substance has a tendency to maintain the fluidity of the albuminoid constituents of the blood, and it assists in preserving the form and consistence of the blood-corpuscles. Its office in nutrition is rather accessory, like that of sodium chloride, than essential, like calcium phosphate, in the constitution of certain structures.

*Origin and Discharge of Sodium Carbonate.*—This substance is not introduced into the body as sodium carbonate, but it is formed, as is calcium carbonate in part, by a decomposition of the malates, tartrates etc., which exist in fruits. It is discharged occasionally in the urine of the human subject, and a great part of it is decomposed in the lungs, carbon dioxide being set free, which latter is discharged in the expired air.

*Potassium Carbonate.*—This salt exists particularly in herbivorous animals. It is found in the human subject under a vegetable diet. Under the heads of uses, origin and discharge, what has been said with regard to sodium carbonate will apply to potassium carbonate.

*Magnesium Carbonate and Sodium Bicarbonate.*—It is most convenient to take up these two salts in connection with the other carbonates, though they are among the least important of the inorganic constituents of the body. Traces of magnesium carbonate have been found in the blood of man, and it exists normally in considerable quantity in the urine of herbivora. In the human subject it is discharged in the sebaceous matter.

Liebig has indicated the presence of sodium bicarbonate in the blood. In this form a certain quantity of carbon dioxide is carried to the lungs, to be exhaled in the expired air.

*Magnesium Phosphate, Sodium Phosphate (neutral) and Potassium Phosphate.*—These salts are found in all the fluids and solids of the body, though not in a very large proportion as compared with calcium phosphate. In their relations to organized structures, they are analogous to calcium phosphate, entering into the composition of the tissues and existing there in a state of intimate combination. They are all taken into the body with food, especially by the carnivora, in the fluids of which they are found in much greater abundance than the carbonates, which latter are in great part the result of the decomposition by carbon dioxide of the malates, tartrates, oxalates etc. With respect to their uses, it can only be said that with calcium phosphate they go to form the organized structures of which they are necessary constituents. They are discharged from the body in the urine and fæces.

*Sodium Sulphate, Potassium Sulphate and Calcium Sulphate.*—Sodium sulphate and potassium sulphate are identical in their situations and apparently in their uses. They are found in all the fluids and solids of the body except in the milk, bile and gastric juice. Their origin in the body is from the food, in which they are contained in small quantity, and they are discharged in the urine. Their chief office appears to be in the blood, where they tend to preserve the fluidity of the albuminoid matters and the form and consistence of the blood-corpuscles. Calcium sulphate is found in the blood and fæces. It is introduced into the body in solution in the water which is used as drink, and it is discharged in the fæces. Its office is not understood and is probably not very important.

*Ammonium Chloride.*—This substance has simply been indicated by chemists as existing in the gastric juice of ruminants, the saliva, tears and urine. It is discharged in the urine, in which it exists in the proportion of 0·41 part per 1,000 (Simon). Its origin and uses are unknown. Various combinations of bases with organic acids taken as food, as the acetates, tartrates etc., found in fruits, undergo decomposition in the body and are transformed into carbonates. In this form they behave precisely like the other inorganic salts.

## SUBSTANCES CONSUMED IN THE ORGANISM.

All of the assimilable organic matters taken as food are consumed in the organism, and none are ever discharged from the body in health in the form in which they entered. The matters thus consumed in nutrition have been divided into nitrogenized and non-nitrogenized; and although they both disappear in the organism, they possess certain marked differences in their properties and probably, also, in their relations to nutrition.

*Nitrogenized Constituents of the Body (Albuminoids).*—The organic constituents of the body are composed of carbon, hydrogen, oxygen, nitrogen and sulphur. The exact proportions of these elements are not definitely fixed, and the nitrogenized matters may change in their general characters without undergoing corresponding changes in their actual ultimate constitution, unless it be in the arrangement of their atoms. They are coagulable and non-crystallizable. They possess certain properties in common with each other, which have already been described more or less fully in connection with the physiological history of the blood, alimentation, the secreted fluids etc. One of these properties is a tendency to decomposition by putrefaction, under certain conditions of heat and moisture. They also undergo certain changes under chemical manipulation, analogous to those already described as effected by the prolonged action of the pancreatic juice. The type of substances of this class is the albumen of white of egg, and as a class, they are generally known as albuminoids. Artificial subdivisions of these substances have been made into proteids and albuminoids, the latter name, in this subdivision, being restricted to certain albuminoids which closely resemble proteids but possess some distinctive characters. Inasmuch as proteine is an hypothetical compound and the so-called proteids do not differ much from other nitrogenized substances, it seems better to designate the entire class as albuminoids.

The so-called proteids are the albuminoid constituents of the blood, lymph and chyle, and the characteristic albuminoid constituents of the various tissues. These are sometimes called colloids. They pass through membranes with difficulty, or are very slightly osmotic. In this regard they present a striking contrast to the peptones, which are very osmotic, passing easily through animal membranes. This distinction is important, and it has already been fully described in connection with the physiology of digestion and absorption.

Nitrogenized matters constitute an important class of alimentary substances, and the corresponding constituents of the body are all originally derived from food. The condition of existence of these substances in the body is always one of union with more or less of the class of inorganic matters. Nitrogenized matters are found in all of the tissues and liquids of the body, except the bile and urine. They undergo changes in digestion before they become a part of the blood, they are changed in the blood into the nitrogenized constituents of this fluid and are again changed as they are deposited in the tissues in the process of nutrition. They are not discharged from the body in health, but are destroyed or changed into excrementitious matters, chiefly urea, and in this form are eliminated in the excretions. An excess of these substances taken as food is not discharged in the fæces, nor does it pass out, in the form in which it entered, in the urine; but it undergoes digestion, becomes absorbed by the blood, and increases the quantity of nitrogenized excrementitious matters discharged, particularly the urea. This fact is shown by the great increase in the elimination of urea produced by an excess of nitrogenized food. Whether the nitrogenized matter that is not actually needed in nutrition be changed into urea in the blood, in the so-called luxus-consumption process, or whether it be appropriated by the tissues, increasing the activity of their disassimilation, is a question difficult to determine experimentally. Certain it is, however, that an excess of nitrogenized food is thrown off in nearly the same way as an excess of inorganic matter; the difference being that the latter passes out in the form in which it has entered, and the former is discharged in the form of nitrogenized excrementitious matters.

The nutrition of the nitrogenized constituents of the tissues may be greatly modified by the supply of new matter. For example, a diet composed of nitrogenized matter in a readily assimilable form will undoubtedly affect favorably the development of the corresponding tissues of the body; and on the other hand, a deficiency in the supply will produce a corresponding diminution in power and development. The modifications in nutrition due to supply have, however, certain well defined limits. As regards the muscular tissue, proper exercise increases nutritive activity, the development and power of muscles and the capacity for muscular work and endurance. The nutritive activity of other parts and organs is limited and is not sensibly affected by an excess of nitrogenized food.

In addition to the albuminoids of the blood, lymph, chyle and secreted fluids, and those which have been described as alimentary matters, the following have been found in various tissues and organs of the body.

Cystalline, a nitrogenized substance in the crystalline lens.

Myosine, a substance extracted from muscular tissue, of which it is the chief nitrogenized constituent.

Keratine, found in the epidermis and its appendages.

Elastine, the nitrogenized constituent of the elastic tissues.

Osseine, in bones, and chondrine, in cartilage.

Gelatine, probably not a normal constituent of the body, but a substance formed from the connective tissues by prolonged boiling in water.

Certain nitrogenized substances containing phosphorus, found in the nervous tissues, which will be described in connection with the chemistry of the nervous system.

The changes involved in nutrition, assimilation, or nutritive metabolism, are apparently dependent upon properties belonging to the nitrogenized constituents of the tissues. When the supply of new matter is equal to the destructive metabolism, the system is in what is called a condition of equilibrium, and the body neither gains nor loses in weight. In growth, the supply exceeds the waste, and in the opposite condition, the waste exceeds the supply.

Certain liquids and tissues of the human body may be restored after their destruction. The blood and its corpuscles undergo regeneration. Blood-vessels, also, may be regenerated, being developed first as capillaries and afterward as arteries and veins. The same is probably true of lymphatics. The epidermis and its appendages and certain parts of the true skin may be regenerated after destruction. Muscular substance, after certain kinds of degeneration in disease, as in fevers, may be restored. Portions of nerves may be regenerated after division or exsection. A divided tendon may become reunited by connective tissue. Portions of cartilage or bone may be regenerated, if the perichondrium or the periosteum remain intact. When wounded or lost parts are not absolutely restored, the divided tissue is reunited or the lost tissue is supplied by what is called cicatricial connective tissue.

*Non-Nitrogenized Constituents of the Body.*—Under the head of alimentation, the general properties of non-nitrogenized matters (starch, sugars and fats) have been fully described. These are important constituents of food, but in themselves they are incapable of supporting life. They are introduced as food, but are destroyed in the organism and are never discharged from the body in health in the form in which they entered.

The carbohydrates (starch and sugars) are all converted into glucose in digestion. As glucose they are taken up by the blood and carried to the liver, where they are in great part and probably entirely converted into glycogen. The glycogen thus formed is stored up in the liver and is gradually transformed into animal sugar, which passes into the blood slowly and gradually, and promptly disappears as sugar, usually in the passage of the blood through the lungs. In addition to the glycogen formed from the carbohydrates of food, the liver is capable of forming glycogen from other substances, as is shown by the presence of glycogen in the liver of carnivorous animals. It is probable that the glycogen thus produced is formed from albuminoid matters and not from fats. The exact mechanism of the destruction of carbohydrates in the organism has not been fully understood, although it is admitted that these substances are important factors in the production of animal heat. The presence of alcohol in very small quantity in the normal blood has been demonstrated by Ford (1872). If this be admitted—and the accuracy of the observations by Ford seems to have been absolute—it is reasonable to suppose that the small quantity of sugar constantly discharged into the blood by the liver is converted into alcohol, which is promptly oxidized, being converted into carbon dioxide and water. The carbohydrates, in contributing to calorification, are very important in saving destruction of the albuminoid constituents of the body. In this process the carbohydrates and the fats act together and in the same way; and in this action they are capable of mutually replacing each other.

The fats taken as food are either consumed in the organism or are deposited in the form of adipose tissue. That the fats are consumed, there can be no doubt; for in the normal alimentation of man, fat is a constant article, and it is never discharged from the body. For a time, during absorption, fat may exist in certain quantity in the blood; but it soon disappears and is either destroyed directly in the circulatory system or is deposited in the form of adipose tissue to supply a certain quantity of this substance consumed. That it may be destroyed directly, is proved by the consumption of fat in instances where the quantity of adipose matter is insignificant; and that the adipose tissue of the organism may be consumed, is shown by its rapid disappearance in starvation.

*Formation and Deposition of Fat.*—The question of the formation of fat in the economy is one of great importance. Whatever the exact nature of the changes accompanying the destruction of non-nitrogenized matters may be, it is certain that the fat stored up in the body is consumed, when there is a deficiency in any of the constituents of food, as well as that which is taken into the alimentary canal. It is rendered probable, indeed, by the few experiments that have been made upon the subject, that obesity increases the power of resistance to inanition. At all events, in starvation, the fatty constituents of the body are the first to be consumed, and they almost entirely disappear before death. Sugar is never deposited in any part of the organism, and it is merely a temporary constituent of the blood. If the sugars and fats have, in certain regards, similar relations to nutrition, and if, in addition to the mechanical uses of fat, it may be retained in the organism for use under extraordinary conditions, it becomes important to ascertain the mechanism of its production and deposition.

The production of fatty matter by certain insects, in excess of the fat supplied with the food, was established long ago by the researches of Huber;

and analogous observations have been made upon birds and mammals, by Boussingault. Under certain conditions more fat exists in the bodies of animals than can be accounted for by the total quantity of fat taken as food added to the fat existing at birth. In experiments with reference to the influence of different kinds of food upon the development of fat, it has been ascertained that fat can be produced in animals upon a regimen sufficiently nitrogenized but deprived of fatty matters; but the fact should be recognized that "the nutriment which produces the most rapid and pronounced fattening is precisely that which joins to the proper proportion of albuminoid substances the greatest proportion of fatty matters" (Boussingault).

There can be no doubt with regard to the formation of fat in the organism from albuminoid matters. Where an excess of such matters is taken as food, it is probable that the albuminoid substance is decomposed, and that a part of it is either deposited as fat or is oxidized into carbon dioxide and water, and a part is discharged from the body in the form of urea.

Theoretical considerations point to starch and sugar as the constituents of food most easily convertible into fat, as they contain the same elements, though in different proportions; and it is more than probable that this view is correct. It is said that in sugar-growing sections, during the time of grinding the cane, the laborers become excessively fat, from eating large quantities of saccharine matter; and although there are no exact scientific observations upon this point, the fact is generally admitted by physiologists. Again, it has been frequently a matter of individual experience that sugar and starch are favorable to the deposition of fat, especially when there is a constitutional tendency to obesity. Carbohydrates added in quantity to a nitrogenized diet favor the formation of fat. The fat may be formed from the carbohydrates either directly (Lawes and Gilbert) or indirectly. If formed indirectly, it is probable that the carbohydrates are oxidized into carbon dioxide and water, and that this saves, to a certain extent, destruction of albuminoids. The albuminoids are split up into fats, which are deposited in the body, and into urea.

Fatty degeneration occurs in tissues during certain retrograde processes. The muscular fibres of the uterus, during the involution of this organ after parturition, become filled with fatty granulations. Long disuse of any part will produce such changes in its power of appropriating nitrogenized matter for its regeneration, that it soon becomes atrophied and altered. A portion of the nitrogenized constituents of the tissue, under these conditions, is changed into fatty matter. The fat is here inert, and it takes the place of the substance that gives to the part its characteristic properties. These changes are observed in muscles and nerves that have been long disused or paralyzed. If the change be not too extensive, the fat may be made to disappear and the part will return to its normal constitution, under appropriate exercise; but frequently the alteration has proceeded so far as to be irremediable and permanent.

It is difficult to explain the tendency to obesity observed in some individuals, which is very often hereditary. Such persons will become fat upon a comparatively low diet, while others deposit but little adipose matter, even when the regimen is abundant. It is to be noted, however, that the former are generally addicted to the use of starchy, saccharine and fatty articles of food, while the latter consume a greater proportion of nitrogenized matter. It is not an uncommon remark that the habit of taking large quantities of liquids favors the formation of fat; but it is not easy to find any scientific basis for such an opinion. The formation of fat by any particular organ or organs in the body has not been determined.

*Condition under which Fat exists in the Organism.*—It is said that fat, combined with phosphorus, is united with nitrogenized matter in the substance of the nervous tissue; but its condition here is not well understood. A small quantity of fat is contained in the blood-corpuscles and is held in solution in the bile; but with these exceptions, fat always exists in the body isolated and uncombined with nitrogenized matter, in the form of granules or globules and of adipose tissue. The three varieties of fat (stearine, palmitine and oleine) are here combined in different proportions, which is the cause of the differences in its consistence in different situations.

*Physiological Anatomy of Adipose Tissue.*—Adipose tissue is found in abundance in the interstices of the subcutaneous areolar tissue, where it is sometimes known as the panniculus adiposus. It is not, however, to be confounded with the so-called cellular or areolar tissue, and is simply associated with it without being one of its essential parts; for the areolar tissue is abundant in certain situations, as the eyelids and scrotum, where there is no adipose matter, and adipose tissue exists sometimes, as in the marrow of the bones, without any areolar tissue.

Adipose tissue is widely distributed in the body and has important mechanical uses. Its anatomical element is a rounded or ovoid vesicle, $\frac{1}{800}$ to $\frac{1}{300}$ of an inch (30 to 80 $\mu$) in diameter, composed of a delicate, structureless membrane, $\frac{1}{25000}$ of an inch (1 $\mu$) thick, enclosing fluid contents. The membrane sometimes presents a small nucleus attached to its inner surface. The contents of the vesicles are a minute quantity of an albuminoid fluid moistening the internal surface of the membrane, and a mixture of oleine, palmitine and stearine, nearly liquid at the temperature of the body but becoming harder on cooling. Little rosettes of acicular crystals of palmitine are frequently observed in the fat-vesicles at a low temperature. The quantity of fat in a man of ordinary development equals about one-twentieth of the weight of the body (Carpenter). The adipose vesicles are collected into little lobules, $\frac{1}{25}$ to $\frac{1}{4}$ of an inch (1 to 6 mm.) in diameter, which are surrounded by a rather wide net-work of capillary blood-vessels. Close examination of these vessels shows that they frequently surround individual fat-cells, in the form of single loops. There is no distribution of nerves or lymphatics to the elements of adipose tissue.

*Conditions which influence Nutrition.*—Physiologists know more concerning the conditions that influence the general process of nutrition than about the nature of the process itself. It will be seen, for example, in studying the nervous system, that there are nerves which regulate, to a certain extent, the nutritive forces. This does not imply that nutrition is effected through the influence of the nerves, but it is the fact that certain nerves, by regulating the supply of blood, and perhaps by other influences, are capable of modifying the nutrition of parts to a very considerable extent.

As regards the influence of exercise upon the development of parts, it has been shown that this is not only desirable but indispensable; and the proper performance of the offices of nearly all parts involves the action of the nervous system. It is true that the separate parts of the organism and the organism as a whole have a limited existence; but it is not true that the change of nitrogenized substances into effete matters—a process that is increased in activity by physiological exercise—consumes, so to speak, a definite amount of the limited life of the parts. Physiological exercise increases disassimilation, but it also increases the activity of nutrition and favors development. It is often said that bodily or mental effort is made always at the expense of a definite amount of vitality and matter consumed. This is partly true, but mainly false. Work involves change into effete matter; but when restricted within physiological limits, it engenders a corresponding activity of nutrition, assuming, of course, that the supply from without be sufficient. Other things being equal, a man would live longer under a system of physiological exercise of every part than if he made the least effort possible. It is, indeed, only by such use of parts, that they can undergo proper development and become the seat of normal nutrition. Notwithstanding all these facts, life is self-limited. Organic substances are constantly undergoing transformation. In the living body, their metabolism is unceasing; and after they are removed from what are termed vital conditions, they change, first losing excitability, and afterward decomposing into matters which, like the products of their disassimilation, are destined to be appropriated by the vegetable kingdom. Nutrition sufficient to supply the physiological decay of parts can not continue indefinitely. The forces in the fecundated ovum lead it through a process of development that requires, in the human subject, more than twenty years for its completion; and when development ceases, no one can say why it becomes arrested, nor can any sufficient reason be given why, with an adequate and appropriate supply of material, a man should not grow indefinitely. When the being is fully developed, and during what is known as adult life, the supply seems to be about equal to the waste; but after this, nutrition gradually becomes deficient, and the deposition of new matter in progressive old age becomes more and more inadequate to supply the place of the nitrogenized substance. There may be at this time, as an exception, a considerable deposition of fat; but the nitrogenized matter is always deficient, and the proportion of inorganic matter combined with it is increased.

There can be little if any doubt that the properties which involve the regeneration or nutrition of parts reside in the organic nitrogenized substance, the inorganic matter being passive, or having purely physical uses. If, therefore, as age advances, the organic matter be gradually losing the power of completely regenerating its substance, and if its proportion be progressively diminishing while the inorganic matter is increasing in quantity, a time will come when some of the organs necessary to life will be unable to perform their office. When this occurs, there is death from old age, or physiological dissolution. This may be a gradual failure of the general process of nutrition or it may occur in some one organ or system that is essential to life.

## Animal Heat and Force.

The processes of nutrition in animals are always attended with the development and maintenance of a bodily temperature that is more or less independent of external conditions. This is true in the lowest as well as the highest animal organizations; and analogous phenomena have been observed in plants. In cold-blooded animals, nutrition may be suspended by a diminished external temperature, and certain of the functions become temporarily arrested, to be resumed when the animal is exposed to a greater heat. This is true, to some extent, in certain warm-blooded animals that periodically pass into a condition of stupor, called hibernation; but in man and most of the warm-blooded animals, the general temperature of the body can undergo but slight variations. The animal heat is nearly the same in cold and in hot climates; and if from any cause the body become incapable of keeping up its temperature when exposed to cold, or of moderating it when exposed to heat, death is the inevitable result.

*Estimated Quantity of Heat produced by the Body.*—In order to express quantities of heat, it is necessary to fix upon some definite quantity to be taken as a heat-unit. In what is to follow, a heat-unit is to be understood as the heat required to raise the temperature of one pound of water 1° Fahr. (pound-degree Fahr.).

It has been calculated that one heat-unit is equal to the force expended in raising one pound 772 feet or 772 pounds one foot (Joule). This force is called a foot-pound. The equivalent of heat in force has been calculated by estimating the heat produced by a certain weight falling through a certain distance, assuming the falling force to be precisely equal to the force which has been used in raising the weight; but physicists have not actually succeeded in so completely converting heat into force as to raise one pound 772 feet or 772 pounds one foot, by the expenditure of one heat-unit.

The heat-unit and its equivalent in force are, of course, differently expressed according to the metric system. When heat-units or foot-pounds are given in the text, the equivalents, according to the metric system, are given in parantheses. These equivalents are as follows:

A heat-unit, according to the metric system, or the heat required to raise the temperature of one kilo. of water one degree C., will be designated as a kilo.-degree C.

One pound-degree = 0·252 kilo.-degree C. One kilo.-degree C. = 3·96 (nearly 4) pound-degrees. A kilogrammetre represents the force required to raise a weight of one kilogramme one metre. One foot-pound = 0·138 kilogrammetre. One kilogrammetre = 7·24 foot-pounds. One pound-degree = 772 foot-pounds. One pound-degree = 106·6 kilogrammetres. One kilo.-

degree C. = 422·25 kilogrammetres. One kilo.-degree C. = 3,057 foot-pounds.

Two methods have been employed in arriving at estimates of the actual quantity of heat produced by the body in a definite time:

1. The direct method consists in placing an animal in a calorimeter and measuring the heat produced, making all necessary corrections. This has been repeatedly done, but the results obtained have been very variable and not entirely satisfactory.

The observations of Senator (1872) seemed to fulfill the necessary experimental conditions; and as an average of five observations made on dogs at rest and fasting, he found a production of about 4·21 heat-units per hour per pound weight of the body (2·34 kilo.-degree C. per kilo.).

J. C. Draper (1872) estimated the heat-production in his own person by immersing the body in water. In this observation, many errors must have escaped correction; but the results agreed remarkably with those obtained by Senator. Deducting 1° Fahr. of heat lost by the body, as shown by a reduction in the general temperature, and imparted to the water—a correction not made by Draper—about 4 heat-units were produced per hour per pound weight of the body (2·22 kilo.-degrees C. per kilo.). According to the estimate of Draper, a man weighing 140 pounds (63·5 kilos.) would produce 13,440 heat-units (3·383 kilo.-degrees C.) in twenty-four hours of repose. This would be equal to 10,375,680 foot-pounds, or about 1,430,000 kilogrammetres.

An important element of inaccuracy in all direct observations and one, indeed, which it seems impossible to correct absolutely, is due to the great variations in heat-production with digestion, conditions of muscular repose or exercise, external temperature etc. Another source of error is the difficulty in estimating the heat lost by the body and not actually produced during the time of the observation. These possible inaccuracies are so important and so evident, that the results of direct observations have not been generally accepted by physiologists.

2. The indirect method consists in estimating the heat represented by oxidation, calculated from the quantity of oxygen consumed in the various processes which result in the production and discharge of carbon dioxide, water, urea etc. These estimates have been compared with the calculated heat-value of the food consumed, and the results very nearly correspond.

According to the estimates of Helmholtz, Ranke and others, by the indirect method, the heat-production is equal to about 2·5 heat-units per hour per pound weight of the body (1·39 kilo.-degree C. per kilo.) In a man weighing 180·4 pounds (82 kilos.) the heat-production in twenty-four hours (Helmholtz) was 10,818 heat-units (2,732 kilo.-degrees C.). According to this estimate, a man weighing 140 pounds (63·5 kilos.) would produce 8,400 heat-units (2,118 kilo.-degrees C.) in twenty-four hours. This would be equal to 6,484,800 foot pounds, or about 894,500 kilogrammetres.

Comparing the results of direct observations, showing a production of about four heat-units per pound per hour (2·22 kilo.-degrees C. per kilo.), with those obtained by the indirect methods, 2·5 heat-units per pound per hour (1·39 kilo.-degree C. per kilo.), it is seen that the indirect estimates give about 37½ per cent. less heat produced than is given by direct estimates. It is on account of this great difference, that writers are at a loss to give definite estimates of the actual quantity of heat produced by the body.

A study of this subject and of the details of observations both direct and indirect has made it evident that the experimental difficulties to be overcome and the unavoidable elements of inaccuracy are greater in the direct than in the indirect method. In comparing the estimates of heat actually produced with the heat value of food—which, of course, is the ultimate source of heat and force in the body—the correspondence is much closer if the indirect estimates be adopted. It therefore seems more in accordance with ascertained facts to adopt the indirect estimates, although this can not be done without reserve. The heat produced, then, is probably equal to about 2·5 heat-units (pound-degrees) per hour per pound weight of the body (nearly 1·4 kilo.-degree C. per kilo.) This is equal to about 8,400 heat-units, or about 2,120 kilo.-degrees C., in twenty-four hours; which is equal to about 6,500,000 foot-pounds, or about 900,000 kilogrammetres.

The normal variations in the production of heat are not absolutely and definitely represented by variations in the actual temperature of the body and by the consumption of oxygen. Muscular work may increase the production of heat 60 per cent. (Hirn) while it increases the consumption of oxygen about 4½ times, a large part of the oxidation being expended in the form of work. The production of heat is diminished in fasting animals (dogs) by nearly 45 per cent. (Senator), after deprivation of food for two days. In old age and in infancy, there is less heat produced than in adult life. The production of heat is less in females than in males and is less during the night than during the day. These points will be touched upon again in connection with the normal variations in the temperature of the body.

*Limits of Variation in the Normal Temperature in Man.*—One of the most common methods of taking the general temperature has been to introduce a registering thermometer into the axilla, reading off the degrees after the mercury has become absolutely stationary. Nearly all observations made in this way agree with the results obtained by Gavarret, who estimated that the temperature in the axilla, in a perfectly healthy adult man, in a temperate climate, ranges between 97·7° and 99·5° Fahr. (36·5° and 37·5° C.). Davy, from a large number of observations upon the temperature under the tongue, fixed the standard, in a temperate climate, at 98° Fahr. (36·67° C.) The axilla and the tongue, however, being more or less exposed to external influences, do not exactly represent the general heat of the organism; but these are the situations, particularly the axilla, in which the temperature is most frequently taken in pathological examinations. As a standard for comparison, it may be assumed that the most common temperature in these situations is 98° Fahr. (36·67° C.) subject to variations, within the limits of health of about 0·5° Fahr. (0·27° C.) below and 1·5° (0·82° Fahr. C.) above.

*Variations with External Temperature.*—The general temperature of the body varies, though within very restricted limits, with extreme changes in climate. The results obtained by Davy, in a large number of observations in temperate and hot climates, show an elevation in the tropics of 0·5° to 3° Fahr. (0·27° to 1·65° C.). It is well known, also, that the human body, the surface being properly protected, is capable of enduring for some minutes a heat greater than that of boiling water. Under these conditions, the animal temperature is raised but slightly, as compared with the intense heat of the surrounding atmosphere. In the observations by Dobson, the temperature was raised to 99·5° Fahr. (37·5° C.) in one instance, 101·5° Fahr. (38·6° C.) in another, and 102° Fahr. (38·9° C.) in a third, when the body was exposed to a heat of more than 212° Fahr. (100° C.). Delaroche and Berger, however, found that the temperature in the mouth could be increased by 3° to 9° Fahr. (1·65° to 5·05° C.) after sixteen minutes of exposure to intense heat. This was for the external parts only; and it is not probable that the temperature of the internal organs ever undergoes such wide variations.

It is difficult to estimate the temperature in persons exposed to intense cold, as in Arctic explorations, because care is always taken to protect the surface of the body as completely as possible; but experiments have shown that the animal heat may be considerably reduced, as a temporary condition, without producing death. In the latter part of the last century, Currie caused the temperature in a man to fall 15° Fahr. (8·25° C.) by immersion in a cold bath; but he could not bring it below 83° Fahr. (28·33° C.) This extreme depression, however, lasted only two or three minutes, and the temperature afterward returned to within a few degrees of the normal standard. The results of experiments show that while the normal variations in the temperature in the human subject, even when exposed to great climatic changes, are very slight, generally not more than two degrees Fahr. (1·1° C.), the body may be exposed for a time to excessive heat or cold, and the extreme limits, consistent with the preservation of life, may be reached. As far as has been ascertained by direct experiment, these limits are about 83° and 107° Fahr. (28·33° and 41·67° C.).

*Variations in Different Parts of the Body.*—The blood becomes slightly lowered in its temperature in passing through the general capillary circulation, but the difference is ordinarily not more than a fraction of a degree. This fact is not opposed to the proposition that animal heat is produced in greatest part in the general capillary system, as one of the results of nutritive action; for the blood circulates with such rapidity that the heat acquired in the capillaries of the internal organs, where little or none is lost, is but slightly diminished before the fluid passes into the arteries, even in circulating through the lungs; and cutaneous evaporation simply moderates the heat acquired in the tissues and keeps it at the proper standard.

Bernard ascertained that the blood is usually 0·36° to 1·8° Fahr. (0·2° to 1° C.) warmer in the hepatic veins than in the aorta. The temperature in the hepatic veins is 0·18° to 1·44° Fahr. (0·1° to 0·8° C.) higher than in the portal veins. These results show that the blood coming from the liver is warmer than in any other part of the body. In a series of experiments by

Breschet and Becquerel, who were among the first to employ thermo-electric apparatus in the study of animal heat, it was found that the cellular tissue was 2·5° to 3·3° Fahr. (1·37° to 1·8° C.) cooler than the muscles. As regards the temperature of the blood in the two sides of the heart, experiments upon the lower animals have been somewhat contradictory; but there is no positive evidence of any considerable change in the temperature of the blood in passing through the lungs in the human subject. In the lower animals, there probably exist no constant differences in temperature in the two sides of the heart. When the loss of heat by the general surface is active, as in animals with a slight covering of hair, the blood generally is cooler in the right cavities; but in animals with a thick covering, that probably lose considerable heat by the pulmonary surface, the blood is cooler in the left side of the heart.

*Variations at Different Periods of Life.*—The most important variations in the temperature of the body at different periods of life are observed in infants just after birth. The body of the infant and of young mammalia removed from the mother presents a diminution in temperature of 1° to 4° Fahr. (0·55° to 2·2° C.). In infancy the ability to resist cold is less than in later years; but after a few days the temperature of the child nearly reaches the standard in the adult, and the variations produced by external conditions are not so great.

W. F. Edwards found that in certain animals, particularly dogs and cats, that are born with the eyes closed and in which the foramen ovale remains open for a few days, the temperature rapidly diminished when they were removed from the body of the mother, and that they then become reduced to a condition approximating that of cold-blooded animals; but after about fifteen days, this change in temperature could not be effected. In dogs just born, the temperature fell, after three or four hours' separation from the mother, to a point but a few degrees above that of the surrounding atmosphere. The views advanced by Edwards are illustrated in instances of premature birth, when the animal heat is much more variable than in infants at term, and in cases of persistence of the foramen ovale.

In adult life there does not appear to be any marked and constant variation in the normal temperature; but in old age, while the actual temperature of the body is not notably reduced, the power of resisting refrigerating influences is diminished very considerably. There are no observations showing any constant differences in the temperature of the body in the sexes; and it may be assumed that in the female the animal heat is modified by the same influences and in the same way as in the male.

*Variations in the Heat of the Body at different Times of the Day etc.*—Although the limits of variation in the animal temperature are not very wide, certain fluctuations are observed, depending upon muscular repose or activity, digestion, sleep etc. It has been ascertained that there are two well marked periods in the day when the heat is at its maximum. These are at eleven A. M. and four P. M.; and while all observations agree upon this point, the observations of Lichtenfels and Fröhlich have shown that these periods are well marked, even when no food is taken. Bärensprung and Ladame have observed that the fall in temperature during the night takes place sleeping or waking; and that when sleep is taken during the day, it does not disturb the period of the maximum, which occurs at about four P. M. According to these experiments, at eleven in the morning, the animal heat is at one of its periods of maximum; it gradually diminishes for two or three hours and is raised again to the maximum at about four in the afternoon, when it again undergoes diminution until the next morning. The variations amount to between 1° and 2·16° Fahr. (0·55° and 1·19° C.). The minimum is always during the night.

The influence of defective nutrition or of inanition upon the heat of the body is very marked. In pigeons the extreme variation in temperature during the day, under normal conditions, was found by Chossat to be 1·3° Fahr. (0·7° C.). During the progress of inanition this variation was increased to 5·9° Fahr. (3·25° C.). with a slight diminution in the absolute temperature, and the periods of minimum temperature were unusually prolonged. Immediately preceding death from starvation, the diminution in temperature became very rapid, the rate being 7° to 11° Fahr. (3·85° to 6° C.) per hour. Death usually occurred when the diminution had amounted to about 30° Fahr. (16·5° C.).

When the surrounding conditions call for the development of an unusual quantity of heat, the diet is always modified, both as regards the quantity and kind of food; but when food is taken in sufficient quantity and is of a kind capable of maintaining proper nutrition, its composition does not affect the general temperature. The temperature of the body, indeed, seems to be uniform in the same climate, even in persons living upon entirely different kinds of food (Davy). Nevertheless, the conditions of external temperature have a remarkable influence upon the diet. It is well known that in the heat of summer, the quantity of meats and fat taken is relatively small, and of the succulent, fresh vegetables and fruits, large, as compared with the diet in the winter; but although the proportion of carbohydrates in many of the fresh vegetables used during a short season of the year is not great, these articles are also deficient in nitrogenized matters. During the winter the ordinary diet, composed of meat, fat, bread, potatoes etc., contains a large proportion of nitrogenized substances as well as a considerable proportion of carbohydrates; and in the summer the proportion of both of these varieties of food is reduced, the more succulent articles taking their place. This is farther illustrated by a comparison of the diet in the torrid or temperate and in the frigid zones. It is stated that the daily ration of the Esquimaux is twelve to fifteen pounds (5·433 to 6·804 kilos.) of meat, about one-third of which is fat. Hayes noted that with a temperature of — 60° to — 70° Fahr. (about — 51° to — 57° C.), there was a continual craving for a strong, animal diet, particularly fatty substances.

The influence of alcoholic beverages upon the animal temperature has been studied chiefly with reference to the question of their use in enabling the system to resist excessive cold. The universal testimony of scientific

Arctic explorers is that the use of alcohol does not enable men to endure a very low temperature for any considerable length of time.

As a rule, when the respiratory activity is physiologically increased—as it is by exercise, bodily or mental, ingestion of food or diminished external temperature—the generation of heat in the body is correspondingly raised; and on the other hand, it is diminished by conditions which physiologically decrease the absorption of oxygen and the exhalation of carbon dioxide. The relations of animal heat to the general process of nutrition are most intimate. Any condition that increases the activity of nutrition and of disassimilation, or even any thing that increases disassimilation alone, will increase the production of heat. The reverse of this proposition is equally true.

Notwithstanding the fact that there is a certain correspondence between the activity of the respiratory processes and the production of heat, this is far from being absolute. It has been shown by Senator that digestion increases heat-production rather more than it increases the exhalation of carbon dioxide. Muscular exertion has been found to increase the quantity of oxygen consumed in very much greater proportion than it increased the heat-production (Hirn). Even adding to the heat produced, the work, reduced to heat-units, the heat-production was about doubled, while the quantity of oxygen consumed was increased about four and a half times.

*Influence of Exercise etc., upon the Heat of the Body.*—The most complete repose of the muscular system is observed during sleep, when hardly any of the muscles are brought into action, except those concerned in tranquil respiration. There is always a notable diminution in the general temperature at this time. In the variations in the heat of the body, the minimum is always during the night; and this is not entirely dependent upon sleep, for a depression in temperature is always observed at that time, even when sleep is avoided. It is a matter of common observation, that one of the most efficient means of resisting the depressing influence of cold is to constantly exercise the muscles; and it is well known that after long exposure to intense cold, the tendency to sleep, which becomes almost irresistible, if yielded to, is followed by a very rapid loss of heat and almost certain death. Muscular exercise increases the production of heat; but the variations in the actual temperature of the body in man, although distinct, are seldom very considerable, for the reason that muscular exertion is generally attended with increased action of the skin, which keeps the heat of the body within restricted limits. In very violent muscular exertion, as in fast running, the increased production of heat may be so rapid that it can not be entirely compensated by evaporation from the skin, and the temperature may rise to 104° Fahr. (40° C.). In about an hour and a half the temperature falls to the normal standard (Billroth, quoted by Landois).

The elevation in temperature that attends muscular action is produced directly in the substance of the muscle (Becquerel and Breschet). Introducing a thermo-electric needle into the biceps of a man who used the arm in sawing wood for five minutes, these physiologists noted an elevation of temperature of nearly two degrees Fahr. (1° C.). The production of heat in the muscular tissue has been observed in experiments with portions of muscle from the frog. Not only was there an absorption of oxygen and exhalation of carbon dioxide after the muscle had been removed from the body of the animal, but an elevation in temperature of about one degree Fahr. (0·55° C.) was noted following contractions artificially excited (Matteucci). Observations upon the influence of mental exertion on the temperature of the body have not been so many, but they are, apparently, no less exact in their results. Davy observed a slight but constant elevation during "excited and sustained attention." Lombard noted an elevation of temperature in the head during mental exertion of various kinds, but it was slight, the highest rise not exceeding 0·05° Fahr. (0·027° C.). According to Burdach, the temperature of the body is increased by the emotions of hope, joy, anger and all exciting passions, while it is diminished by fear, fright and mental distress.

It is evident that if animal heat be one of the necessary, attendant phenomena of nutrition, it must be greatly influenced by conditions of the circulation. It has been a question, indeed, whether the modifications in temperature, produced by operating upon the vaso-motor nerves, be not due entirely to changes in the supply of blood. It is certain that whatever determines an increased supply of blood to any part raises the temperature; and whenever the quantity of blood in any organ or part is considerably diminished, the temperature is reduced. This fact is constantly illustrated in operations for the deligation of large arteries. It is well known that after tying a large vessel, the utmost care is necessary to keep up the temperature of the part to which its branches are distributed, until the anastomosing vessels become enlarged sufficiently to supply the quantity of blood necessary for healthy nutrition.

*Influence of the Nervous System upon the Production of Animal Heat* (*Heat-Centres*).—The local influences of the vaso-motor nerves upon calorification operate mainly if not entirely through changes in the nutrition of parts, produced by variations in blood-supply. These influences will be fully considered in connection with the physiology of the nervous system.

The general temperature of the body may be modified through the nervous system by reflex action, and this implies the existence of nerve-centres, or of a nerve-centre, capable of influencing the general process of calorification. Experiments have been made, chiefly on parts of the encephalon, with the view of determining the existence and location of heat-centres. In a recent publication by Ott (1887), four heat-centres are recognized, irritation of which by puncture increases the temperature of the body in rabbits by several degrees (4° to 6° Fahr., or 2·2° to 3·3° C.). These four centres are as follows: 1, in front of and beneath the corpus striatum (Ott); 2, the median portion of the corpora striata and the subjacent parts (Aronsohn and Sachs); 3, between the corpus striatum and the optic thalamus (Ott); 4, the anterior inner end of the optic thalamus (Ott). Puncture of these parts is followed by rise in temperature, which continues for a variable time, two to four days. A similar centre has been described as existing in the dog, in the cortex of the anterior portion of the upper surface of the brain, near the median line (Eulenberg and Landois). The conductors connected with these centres decussate and pass through the medulla oblongata and the spinal cord. The question arises as to whether the effects of puncture or stimulation of these parts be exciting or inhibitory; but observations regarding the mechanism of their action have not been sufficiently definite to warrant any positive conclusions on this point.

### Mechanism of the Production of Animal Heat.

The definite ideas of physiologists concerning the mechanism of the production of heat by animals date from the researches of Lavoisier (1777 to 1790). As a general result of these observations, Lavoisier concluded that animal heat was produced by an internal combustion resulting in carbon dioxide and water. Even now there is little to be said beyond this, as regards the general mechanism of animal calorification, although modern investigations have brought to light many important details in the heat-producing processes.

In man and in the warm-blooded animals generally, the maintenance of the temperature of the organism at a nearly fixed standard is a necessity of life; and while heat is generated in the organism with an activity that is constantly varying, it is counterbalanced by physiological loss of heat from the cutaneous and respiratory surfaces. Variations in the activity of calorification are not to be measured by corresponding changes in the temperature of the body, but are to be estimated by calculating the quantity of heat lost. The ability of the human race to live in all climates is explained by the adaptability of man to different conditions of diet and exercise, and by the power of regulating loss of heat from the surface by appropriate clothing.

Heat is produced in the general system and not in any particular organ or in the blood as it circulates. The experiments of Matteucci, showing an elevation of temperature in a muscle excited to contraction after it had been removed from the body, and the observations of Becquerel and Breschet, showing increased development of heat by muscular contraction, are sufficient evidence of the production of heat in the muscular system; and inasmuch as the muscles constitute by far the greatest part of the weight of the body, they are a most important source of animal heat. It has been observed that the blood becomes notably warmer in passing through the abdominal viscera (Bernard). This is particularly marked in the liver, and it shows that the large and highly organized viscera are also important sources of caloric.

As far as it is possible to determine by experiment, not only is there no particular part or organ in the body endowed with the special office of calorification, but every part in which the nutritive forces are in operation produces a certain quantity of heat; and this is probably true of the blood-corpuscles and other anatomical elements of this class. The production of heat in the body is general and is one of the necessary consequences of the process of nutrition; but, with nutrition, it is subject to local variations, as is illustrated in the effects of operations upon the vaso-motor nerves and in the phenomena of inflammation.

Nutrition and disassimilation involve the appropriation of matters taken into the body and the production and discharge of effete substances. In its widest signification, this includes the consumption of oxygen and the elimination of carbon dioxide; and consequently, respiration may be regarded as a nutritive act. All of the nutritive processes go on together, and they all involve, in most warm-blooded animals at least, a nearly uniform temperature. During the first periods of intraüterine life, the heat derived from the mother is undoubtedly necessary to the development of tissue by a change of substance, analogous to nutrition and even superior to it in activity. During adult life, animal heat and the nutritive force are co-existent. It now becomes an important question to determine whether there be any class of nutritive matters specially concerned in calorification or any nutritive acts exclusively or specially directed to the maintenance of the normal temperature of the body.

It is evident that in normal nutrition by food, the heat of the body must be maintained by changes which take place, either directly in the blood or indirectly in the tissues, in alimentary matters, and that these changes involve oxidation to a very considerable extent. Under ordinary conditions of nutrition, it is assumed that the food furnishes all the material for maintaining the heat of the body and for the development of force in work, such as the muscular work of respiration and circulation and general muscular effort. If no food be taken for a certain time, the heat of the body must be maintained, the work must be accomplished at the expense of the substance of the body itself, and the individual loses weight. In order to maintain the equilibrium of the body, therefore, food should be taken in quantity sufficient to supply, by its changes in oxidation etc., the heat and force required. In this condition of equilibrium, the body neither gains nor loses weight. To furnish a positive scientific basis for calculations with reference to these points, physiologists have burned various articles of food in oxygen, and have estimated their heat-value in heat-units.

In 1866, Frankland made a number of calculations of the heat-units and the estimated force-value of various articles of food, which are now accepted and used by most writers upon subjects connected with the theories of animal heat and the source of muscular power. As regards the heat produced by the oxidation of these substances in the body, if it be assumed that the same quantity of heat is produced by the oxidation, under all circumstances, of a definite quantity of oxidizable matter, it is necessary simply to deduct from the heat-value of articles of food the heat-value remaining in certain parts of the food which pass out of the body in an unoxidized state. It was in this way that Frankland arrived at a determination of the heat-value of articles of food oxidized in the body.

The following selections from Frankland's table will give an idea of the heat-value of different articles of food oxidized in the body. In this table the heat-units are calculated as pound-degrees.

HEAT-VALUE OF TEN GRAINS OF THE MATERIAL OXIDIZED INTO CARBON DIOXIDE, WATER AND UREA IN THE ANIMAL BODY (FRANKLAND).

| Articles of food. | Heat-units. | Articles of food. | Heat-units. |
|---|---|---|---|
| Butter | 18·68 | Potatoes | 2·56 |
| Beef-fat (dry) | 23·33 | Cabbage | 1·08 |
| Lump-sugar | 8·61 | Milk | 1·64 |
| Grape-sugar | 8·42 | Egg (boiled) | 5·86 |
| Wheat-flour | 9·87 | Cheese | 11·20 |
| Bread-crumb | 5·52 | Lean beef | 3·66 |
| Arrowroot | 10·06 | Ham (boiled) | 4·30 |
| Ground rice | 9·52 | Mackerel | 4·14 |

In the following, selected from the table quoted by Chapman, the heat-units are calculated as kilo.-degrees C.

HEAT-VALUE OF ONE GRAMME OF THE MATERIAL OXIDIZED INTO CARBON DIOXIDE, WATER AND UREA IN THE ANIMAL BODY (FRANKLAND).

| Articles of food. | Heat-units. | Articles of food. | Heat-units. |
|---|---|---|---|
| Butter | 7·264 | Potatoes | 0·990 |
| Beef-fat (dry) | 9·069 | Cabbage | 0·420 |
| Lump-sugar | 3·348 | Milk | 0·620 |
| Grape-sugar | 3·227 | Egg (boiled) | 2·280 |
| Wheat-flour | 3·840 | Cheese | 4·360 |
| Bread-crumb | 1·450 | Lean beef | 1·420 |
| Arrowroot | 3·912 | Ham (boiled) | 1·680 |
| Ground rice | 3·760 | Mackerel | 1·610 |

The heat-value of one gramme of alcohol—taken from a table compiled by Landois—is equal to 8·958 heat-units (kilo.-degrees C.), or the heat-value of 10 grains of alcohol is equal to 23 heat-units (pound-degrees Fahr.).

As regards the processes of combustion which take place in the living organism, the oxidation of the constituents of food produces carbon dioxide and water, but it is probable that the quantity of heat produced bears a definite relation to the total consumption of oxygen, the heat, as far as this is concerned, being the same whether the oxygen unite with carbon or with hydrogen (Pflüger). This relation between the quantity of oxygen consumed and the production of heat seems to be disturbed by muscular exercise; but it has thus far been found impossible to estimate accurately the quantity of heat represented by the force expended in muscular work, circulation, respiration etc.

The heat-producing processes undoubtedly are represented mainly by the exhalation of carbon dioxide and water, and to a less degree by the discharge of urea, the quantity of heat produced by other chemical processes being comparatively small. It is also true that the carbohydrates and fats are more important factors in calorification than the albuminoids; but it seems beyond question that there must be heat evolved in the body by oxidation of nitrogenized matters. When the daily quantity of food is largely increased for the purpose of generating the immense quantity of heat required in excessively cold climates, the nitrogenized matters are taken in greater quantity, as well as the fats, although their increase is not in the same proportion. From these facts, and from other considerations that have already been fully discussed, it is evident that the physiological metamorphoses of nitrogenized matters bear a certain share in the production of animal heat. The carbohydrates and fats are not concerned in the building up of tissues and organs, except as the fats are deposited in the form of adipose tissue. Their addition to the food saves the nitrogenized tissues, which latter must be used in heat-production in starvation and in a restricted diet deficient in non-nitrogenized matters. If the non-nitrogenized constituents of food do not form tissue, are not discharged from the body, and are consumed in some of the processes of nutrition, it would seem that their change must involve the production of carbon dioxide and water and the evolution of heat.

Although it may be assumed that the non-nitrogenized constituents of food are particularly important in the production of animal heat, and that they are not concerned in the repair of tissue, it must be remembered that the animal temperature may be kept at the proper standard upon a nitrogenized diet; and it is not possible to connect calorification exclusively with the consumption of any single class of alimentary matters or with any single one of the acts of nutrition.

The exact mechanism of the oxidation-processes in the body is not understood. All physiologists, however, are agreed that the quantity of heat produced by oxidation is the same, whether the combustion be rapid or slow. The fact that fats are never discharged, but are either consumed entirely or are deposited in the body as fat, leaves their oxidation and discharge as oxidation-products the only alternative. The oxidation of albuminoids has already been considered. As regards the carbohydrates, if it can be shown that alcohol normally exists in the blood, even in very small quantity, the idea that these matters are slowly passed from the liver as sugar, into the general circulation, and are then converted into alcohol which is promptly oxidized, is worthy of serious consideration. Such a theory would explain the destination of the carbohydrates and their relations to calorification. There can be no doubt that in certain cases of fever, alcohol administered in large quantity may be oxidized and "feed" the fever, thus saving consumption of tissue.

In a series of observations made in 1879 (Flint), it seemed impossible to account for the heat actually produced in the body and expended as force in muscular work etc., by the heat-value of food and of tissue consumed. The estimates of heat-production, made by the direct method, were then adopted; but even the indirect estimates, which were much less, presented difficulty, though in a less degree. In these observations, it was shown that water was actually produced in the body in quantity over and above that contained in food and drink, during severe and prolonged muscular exertion. It was also shown that water was produced in considerable quantity during twenty-four hours of abstinence from food. It has been shown by Pettenkofer and Voit that "the elimination of water is very much increased by work, and the increase continues during the ensuing hours of sleep." As regards the oxidation of hydrogen in this formation of water, it is probable that the hydrogen of the tissues is used and that the matter thus consumed is supplied again to the tissues in order to maintain the physiological *status* of the organism. Adding the heat-value of the water thus produced to the heat-value of food, there is little difficulty in accounting for the heat and force actually produced and expended.

The demonstration that water is actually formed within the organism, under certain conditions, not only completes the oxidation-theory of the production of animal heat, but it affords an explanation of certain physiological phenomena that have been heretofore obscure. It is well known, for example, that a proper system of physical training will reduce the fat of the body to a minimum consistent with health and strength. This involves a diet containing a relatively small proportion of fat and liquids, and regular muscular exercise attended with profuse sweating. Muscular work increases the elimination of water, while it also exaggerates for the time the calorific processes. Muscular exercise undoubtedly favors the consumption of the non-nitrogenized parts of the body, and a diminution of the supply of fats, carbohydrates and water in the food prevents, to a certain extent, the new formation of fat. In excessive muscular exertion, the production of water is increased and the circulation becomes more active. The volume of blood then circulating in the skin and passing through the lungs in a given time is relatively increased, and there is an increased discharge of water from these surfaces. The same condition that produces an increased quantity of water in the body and has a tendency to exaggerate the process of calorification seems to produce also an increased evaporation from the surface, which serves to equalize the animal temperature.

*Equalization of the Animal Temperature.*—A study of the phenomena of calorification in the human subject has shown that under all conditions of climate the general heat of the body is equalized. There is always more or less loss of heat by evaporation from the general surface, and when the surrounding atmosphere is very cold, it becomes desirable to reduce this loss to the minimum. This is done by appropriate clothing, which must certainly be regarded as a physiological necessity. Clothing protects from excessive heat as well as from cold. Thin, porous articles moderate the heat of the sun, equalize evaporation and afford great protection in hot climates. In excessive cold, clothing moderates the loss of heat from the surface. When the body is not exposed to currents of air, garments are useful chiefly as non-conductors, imprisoning many layers of air, which are warmed by contact with the person. It is also important to protect the body from the wind, which greatly increases the loss of heat by evaporation.

When from any cause there is a tendency to undue elevation of the heat of the body, cutaneous transpiration is increased, and the temperature is kept at the proper standard. This has already been considered in treating of the action of the skin, and facts were noted showing that men can work when exposed to a heat much higher than that of the body itself. The quantity of vapor that is lost under these conditions is sometimes very large.

Tillet recorded an instance of a young girl who remained in an oven for ten minutes without inconvenience, at a temperature of 324·5° Fahr. (162·5° C.). Blagden, in his noted experiments in a heated room, made in connection with Banks, Solander, Fordyce, and others, found in one series of observations, that a temperature of 211° Fahr. (99·5° C.) could be easily borne; and at another time the heat was raised to 260° Fahr. (126·5° C.). Under these extraordinary external conditions, the body is protected from the radiated heat by clothing, the air is perfectly dry, and the animal temperature is kept down by increased evaporation from the surface.

It is a curious fact that after exposure of the body to an intense, dry heat or to a heated vapor, as in the Turkish or Russian baths, when the general temperature is somewhat raised and the surface is bathed in perspiration, a cold plunge, which checks the action of the skin almost immediately, is not injurious and is decidedly agreeable. This presents a striking contrast to the effects of sudden cold upon a system heated and exhausted by long-continued exertion. In the latter instance, when the perspiration is suddenly checked, serious disorders of nutrition, with inflammation etc., are liable to occur. The explanation of this seems to be the following: When the skin acts to keep down the temperature of the body in simple exposure to external heat, there is no modification in nutrition, and the tendency to an elevation of the animal temperature comes from causes entirely external. It is a practical observation that no ill effects are produced, under these circumstances, by suddenly changing the external conditions; but when the animal temperature is raised by a modification of the internal nutritive processes, as in prolonged muscular effort, these changes should not be suddenly arrested; and a suppression of the compensative action of the skin is liable to produce disturbances in nutrition, often resulting in inflammations.

## Relations of Heat to Force.

Since the development of the theory of the conservation of forces, which had its origin in an essay published by J. R. Mayer, in 1842, physiologists have applied the laws of correlation and conservation of forces to operations involving the production of heat and the development and expenditure of force in animals. This theory, if applicable to what were formerly called vital operations, certainly affords, in its definite quantities of heat and force as expressed in heat-units and foot-pounds, a basis for calculating the absolute value of material changes in the body. Without discussing the purely physical questions involved, the laws of correlation and conservation of forces, as they are applicable to human physiology, may be briefly stated as follows:

Potential energy is something either residing in or imparted to matter, which is capable of being converted directly or indirectly into heat. The animal body, for example, is a store-house of potential energy. Its tissues may be made to unite with oxygen and heat is produced. Any body may have potential energy imparted to it. If a weight be raised to a certain height, when the force which has accomplished this work is exhausted, the potential energy imparted to the weight causes it to fall, and in this fall, heat is produced. The weight may be supported at the height to which it has been raised, for an indefinite time; but it still possesses the potential energy which has been imparted to it, and when the support is removed, this potential energy is converted into force which may be converted into heat. Potential energy may be converted directly into heat, as when a body is oxidized. It is converted indirectly into heat, when movement, falling or other force is produced, for all force may be converted into heat. This conversion into heat, directly or indirectly, affords a convenient measure of potential energy. Using the example of the change of potential energy into heat by oxidation, the energy stored up in matter is measured by estimating the heat produced by oxidation, as so many heat-units. Using the example of falling force imparted to a weight, the potential energy imparted to the body is estimated by calculating the heat produced by the body falling.

If the entire body of an animal were burned in a calorimeter, the heat produced would be an exact measure of the potential energy of the tissues, converted into heat by oxidation. If one can imagine an animal perfectly quiescent, neither losing nor gaining weight, nourished by food, expending no force in circulation and respiration, but supplied with oxygen, the potential energy of the food could be measured by the heat produced. In animal organisms, heat is produced mainly by oxidation, although other chemical processes contribute to the production of heat, to some extent. The body contains the potential energy stored up in its tissues. The oxygen taken in by respiration changes a certain part of this potential energy into heat. If food be not supplied in adequate quantity, the body loses weight by this change of tissue into certain matters, such as carbon dioxide, water and urea, which are discharged. Food supplies the waste of tissue and is the ultimate source of the potential energy of the body. If food be supplied in excess, that which is not in some form discharged from the body remains and adds to the total potential energy stored up in the organism.

Kinetic energy is mechanical force. It is the force of a falling body, or as regards animal mechanics, it is muscular force used in respiration, circulation or any kind of muscular work. In physics, kinetic energy, or force, and heat are regarded as mutually convertible. The reasoning by which this law was formulated is the following:

The force used in raising a weight to a certain height, which is imparted to the weight as potential energy, is precisely equal to the force developed by this body as it falls. If this force could be transmitted to another body of equal weight, without any expenditure of energy in friction, it would raise the second weight to an equal height. The arbitrary unit of this force is a foot-pound or a kilogrammetre, terms which have already been defined. The falling of a body of a certain weight through a definite distance produces a definite quantity of heat that itself is capable of producing force; and it is assumed that the heat produced by a falling body, if absolutely and entirely converted into force, would raise that body to the height from which it had fallen, or would exactly equal the falling force. A heat-unit is therefore said to be equal to a definite number of foot-pounds or kilogrammetres. Calculations have been made showing the conversion of foot-pounds or kilogrammetres into heat-units, but mechanical difficulties have thus far prevented the actual conversion of heat-units into their equivalents in foot-pounds or kilogrammetres. As a matter of reasoning, however, it is assumed that if a certain number of foot-pounds or kilogrammetres be equal to a certain number of heat-units, the reverse of the equation is true; but in the application of this law to animal physiology, it is always by a conversion of heat-units into foot-pounds or kilogrammetres. The experiments on which the law rests have been made by converting foot-pounds or kilogrammetres into heat-units.

In work by machinery a very large proportion of the force-value of fuel is dissipated in the form of heat. This is well illustrated by Landois. If a steam-engine burning a certain quantity of coal, but doing no work, be placed in a calorimeter, the heat produced can be measured. If, now, the engine be made to do a certain work, as in raising a weight, the heat, as measured by the calorimeter, will be less and the work done is found to be very nearly proportional to the decrease in the measured heat (Hirn). It is estimated by Landois, that of the heat produced by the body, one-fifth may be used as work. In the best steam-engine, it is possible to use only one-eighth as work, seven-eighths being dissipated as heat.

Many elaborate and careful estimates have been made of the mechanical work produced by the human body. The basis of such calculations is more or less indefinite, and the reduction of the work to foot-pounds or kilogrammetres is difficult and inexact. Even the general statement, that of the heat-units produced by the body, four-fifths remain as heat and one-fifth is converted into work, must be regarded as merely approximate.

In the animal organism, a part of the potential energy of the tissues may be converted into force by voluntary effort. In fevers, an abnormally large proportion of the potential energy of the organism is converted into heat, and it is not possible to use much of this energy as force. These and other peculiarities of living bodies, as regards the production of heat and force, are difficult of explanation. In the essential fevers, the conditions which involve the abnormal production of heat finally consume the substance of the tissues. They involve especially an increased production of carbon dioxide and urea and not to any great extent the formation of water. If heat-producing alimentary substances and alcohol can be introduced and consumed, the tissues are thereby proportionally saved from destruction and degenerations.

# CHAPTER XV.

## *MOVEMENTS—VOICE AND SPEECH.*

Amorphous contractile substance and amœboid movements—Ciliary movements—Movements due to elasticity—Elastic tissue—Muscular movements—Physiological anatomy of the involuntary muscular tissue—Contraction of the involuntary muscular tissue—Physiological anatomy of the voluntary muscular tissue—Connective tissue—Connection of the muscles with the tendons—Chemical composition of the muscles—Physiological properties of the muscles—Muscular contractility, or excitability—Muscular contraction—Electric phenomena in muscles—Muscular effort—Passive organs of locomotion—Physiological anatomy of the bones—Physiological anatomy of cartilage—Voice and speech—Sketch of the physiological anatomy of the vocal organs—Mechanism of the production of the voice—Laryngeal mechanism of the vocal registers—Mechanism of speech—The phonograph.

THE various processes connected with the nutrition of animals involve certain movements; and almost all animals possess in addition the power of locomotion. Many of these movements have of necessity been considered in connection with the different functions; as the action of the heart and vessels in the circulation, the uses of the muscles in respiration, the ciliary movements in the air-passages, the muscular acts in deglutition, the peristaltic movements and the mechanism of defæcation and urination. There remain, however, certain general facts with regard to various kinds of movement and the mode of action of the different varieties of muscular tissue, that will demand more or less extended consideration. As regards the varied and complex acts concerned in locomotion, it is difficult to fix a limit between anatomy and physiology. A full comprehension of such movements should be preceded by a complete descriptive anatomical account of the passive and active organs of locomotion; and special treatises on anatomy give the uses and actions as well as the structure and relations of these parts.

*Amorphous Contractile Substance and Amœboid Movements.*—In some of the lowest forms of beings, in which hardly any thing but amorphous matter and a few granules can be recognized by the microscope, certain movements of elongation and retraction of their amorphous substance have been observed. In the higher animals, similar movements have been noticed in certain of their structures, such as the leucocytes, the contents of the ovum, epithelial cells and connective-tissue cells. These movements generally are simple changes in the form of the cell, nucleus, or whatever it may be. They depend upon an organic principle formerly called sarcode and now known as protoplasm; but it is not known that such movements are characteristic of any one definite constituent of the body, nor is it easy to determine their cause and their physiological importance. In the anatomical elements of adult animals of the higher classes, these movements usually appear slow and gradual, even when viewed with high magnifying powers; but in some of the very lowest forms of life, these movements

FIG. 142.—*Amœba diffluens, changing in form and moving in the direction indicated by the arrow* (Longet).

serve as a means of progression and are more rapid. Such movements are called amœboid. It does not seem possible to explain the nature and cause of the movements of homogeneous contractile substance; and it must be excessively difficult, if not impossible, to observe directly the effects of different stimuli, in the manner in which the movements of muscles are studied. They seem to be analogous to the ciliary movements, the cause of which is equally obscure.

*Ciliary Movements.*—The epithelium covering certain of the mucous membranes is provided with little, hair-like processes upon the borders of the cells, called cilia. These are in constant motion, from the beginning to the end of life, and they produce currents upon the surfaces of the membranes to which they are attached, the direction being generally from within outward. In man and in the warm-blooded animals generally, the ciliated or vibratile epithelium is of the variety called columnar, conoidal or prismoidal. The cilia are attached to the thick ends of the cells, and they form on the surface of the membrane a continuous sheet of vibrating processes. In general structure the ciliary processes are entirely homogeneous, and they gradually taper from their attachment to the cell to an extremity of excessive tenuity.

The presence of cilia has been demonstrated upon the following surfaces: The respiratory passages, including the nasal fossæ, the pituitary membrane, the summit of the larynx, the bronchial tubes, the superior surface of the velum palati and the Eustachian tubes; the sinuses about the head; the lachrymal sac and the internal surface of the eyelids; the genital passages of the female, from the middle of the neck of the uterus to the fimbriated extremities of the Fallopian tubes; the ventricles of the brain. In these situations, on each cell of conoidal epithelium are six to twelve prolongations, about $\frac{1}{25000}$ of an inch (1 $\mu$) in thickness at their base, and $\frac{1}{5000}$ to $\frac{1}{4000}$ of an inch (5 to 6 $\mu$) in length. Between the cilia and the substance of the cell, there is usually a thin, transparent disk. The appearance of the cilia is represented in Fig. 143. When seen *in situ*, they appear regularly disposed upon the surface, are of nearly equal length and are generally slightly inclined in the direction of the opening of the cavity lined by the membrane.

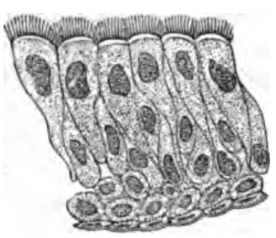

FIG. 143.—*Ciliated epithelium* (Landois).

When the ciliary movements are seen in a large number of cells *in situ*, the appearance is well illustrated by the comparison by Henle to the undulations of a field of wheat agitated by the wind. In watching this movement, it is usually seen to gradually diminish in rapidity, until what at first appeared simply as currents, produced by movements too rapid to be studied in detail, become revealed as distinct undulations, in which the action of individual cilia can be readily studied. Several kinds of movement have been described, but the most common is a bending of the cilia, simultaneously or in regular succession, in one direction, followed by an undulating return to the perpendicular. The other movements, such as the infundibuliform, in which the point describes a circle around the base, the pendulum-movement etc., are not common and are unimportant.

The combined action of the cilia upon the surface of a mucous membrane, moving as they do in one direction, is to produce currents of considerable power. This may be illustrated under the microscope by covering the surface with a liquid holding little, solid particles in suspension; when the granules are tossed from one portion of the field to another, with considerable force. It is not difficult, indeed, to measure in this way the rapidity of the ciliary currents. In the frog it has been estimated at $\frac{1}{250}$ to $\frac{1}{175}$ of an inch (100 to 140 $\mu$) per second, the number of vibratile movements being seventy-five to one hundred and fifty per minute. In the fresh-water polyp the movements are more rapid, being two hundred and fifty or three hundred per minute. There is no reliable estimate of the rapidity of the ciliary currents in man, but they are probably more active than in animals low in the scale.

The movements of cilia, like those observed in fully developed spermatozoids, seem to be independent of nervous influence, and they are affected only by local conditions. They will continue, under favorable circumstances, for more than twenty-four hours after death, and they can be seen in cells entirely detached from the body when they are moistened with proper fluids. When the cells are moistened with pure water, the activity of the movement is at first increased; but it soon disappears as the cells become swollen. Acids arrest the movement, but it may be excited by feebly alkaline solutions. There seems to be no possibility of explaining the movement except by a simple statement of the fact that the cilia have the property of moving in a certain way so long as they are under normal conditions. As regards the physiological uses of these movements, it is sufficient to refer to the physiology of the parts in which cilia are found, where the peculiarities of their action are considered more in detail. In the lungs and the air-passages generally and in the genital passages of the female, the currents are of considerable importance; but it is difficult to imagine the use of these movements in certain other situations, as the ventricles of the brain.

*Movements due to Elasticity.*—There are certain important movements in the body that are due simply to the action of elastic ligaments or membranes. These are distinct from muscular movements, and are not even to be classed with the movements produced by the resiliency of muscular tissue, in which muscular tonicity is more or less involved. Movements of this kind consist simply in the return of movable parts to a certain position after they have been displaced by muscular action, and in the reaction of tubes after forcible distention, as in the walls of the large arteries.

*Elastic Tissue.*—Most anatomists adopt the division of the elements of elastic tissue into three varieties. This division relates to the size of the fibres; and all varieties are found to possess essentially the same chemical composition and general properties. On account of the yellow color of this tissue, presenting, as it does, a strong contrast to the white, glistening appearance of the inelastic fibres, it is frequently called the yellow, elastic tissue.

The first variety of elastic tissue is composed of small fibres, generally intermingled with fibres of the ordinary inelastic tissue. They possess all the chemical and physical characters of the larger fibres, but are very fine, measuring $\frac{1}{25000}$ to $\frac{1}{6000}$ or $\frac{1}{5000}$ of an inch (1 to 4 or 5 $\mu$) in diameter. If acetic acid be added to a preparation of ordinary connective tissue, the inelastic fibres are rendered semi-transparent, but the elastic fibres are unaffected and become quite distinct. They are then seen isolated, that is, never arranged in bundles, generally with a dark, double contour, branching, brittle, and when broken, their extremities curled and presenting a sharp fracture, like a piece of India-rubber. These fibres pursue a wavy course between the bundles of inelastic fibres in the areolar tissue and in most of the ordinary fibrous membranes. They are found in greater or less abundance in the situations just mentioned; in the ligaments, but not the tendons; in the layers of non-striated muscular tissue; the true skin; the true vocal chords; the trachea, bronchial tubes, and largely in the parenchyma of the lungs; the external layer of the large arteries; and, in brief, in nearly all situations in which the ordinary connective tissue exists.

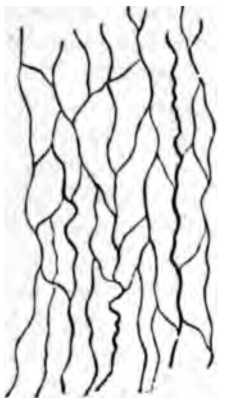

FIG. 144.—*Small elastic fibres from the peritoneum; magnified 850 diameters* (Kölliker).

FIG. 145.—*Larger elastic fibres* (Robin).

The second variety of elastic tissue is composed of fibres, larger than the first, ribbon-shaped, with well-defined outlines, anatomosing, undulating or curved in the form of the letter S, presenting the same curled ends and sharp fracture as the smaller fibres. These measure $\frac{1}{5000}$ to $\frac{1}{3000}$ of an inch (5 to 8 $\mu$) in diameter. Their type is found in the ligamenta subflava and the ligamentum nuchæ. They are also found in some of the ligaments of the larynx, the stylo-hyoid ligament and the suspensory ligament of the penis.

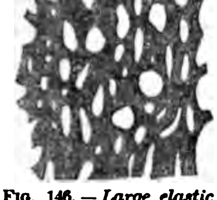

FIG. 146. — *Large elastic fibres (fenestrated membrane), from the middle coat of the carotid of the horse; magnified 850 diameters* (Kölliker).

The third variety of elastic tissue is found forming the middle coat of the large arteries, and it has already been described in connection with the vascular system. The fibres are large and flat, inosculating freely with each other by short, communicating branches. These anastomosing fibres, forming the so-called fenestrated membranes, are arranged in layers, and the structure is sometimes called the lamellar elastic tissue.

The great resistance which the elastic tissue presents to chemical action serves to distinguish it from nearly every other structure in the body. It is not affected by acetic acid or by boiling with sodium hydrate. It is not softened by prolonged boiling in water, but it is slowly dissolved, without decomposition, by sulphuric, nitric or hydrochloric acid, the solution not being precipitable by potassium hydrate. Its organic constituent is a nitrogenized substance called elastine, containing carbon, hydrogen, oxygen and nitrogen, without sulphur. This is supposed to be identical with the sarcolemma of the muscular tissue.

The purely physical property of elasticity plays an important part in many of the animal functions. Examples of this are in the action of the large arteries in the circulation, and in the resiliency of the parenchyma of the lungs. The ligamenta subflava and the ligamentum nuchæ are important in aiding to maintain the erect position of the body and head and to restore this position when flexion has been produced by muscular action. Still, the contraction of muscles also is necessary to keep the body in a vertical position.

## Muscular Movements.

The muscular movements are divided into voluntary and involuntary; and generally there is a corresponding division of the muscles as regards their minute anatomy. The latter, however, is not absolute; for there are certain involuntary actions, like the contractions of the heart or the movements of deglutition, that require the rapid, vigorous contraction characteristic of the voluntary muscular tissue, and here the structure resembles that of the voluntary muscles. With a few exceptions, however, the anatomical division of the muscular tissue into voluntary and involuntary is sufficiently distinct.

*Physiological Anatomy of the Involuntary Muscular Tissue.*—The involuntary muscular system presents a striking contrast to the voluntary muscles, not only in its minute anatomy and mode of action, but in the arrangement of its fibres. While the voluntary muscles are almost invariably attached by their extremities to movable parts, the involuntary muscles form sheets or membranes in the walls of hollow organs, and by their contraction, they simply modify the capacity of the cavities which they surround. On account of the peculiar structure of the fibres, they have been called muscular fibre-cells, smooth muscular fibres, pale fibres, non-striated fibres, fusiform fibres and contractile cells. The distribution of these fibres to parts concerned in the organic functions, as the alimentary canal, has given them the name of organic muscular fibres, or fibres of organic life. In their natural condition, the involuntary muscular fibres are pale, finely granular, flattened, and of an elongated spindle-shape, with a very long, narrow, almost linear nucleus in the centre. The nucleus generally has no distinct nucleolus, and it is sometimes curved or shaped like the letter S. The ordinary length of these fibres is about $\frac{1}{500}$ (50 $\mu$) and their breadth, about $\frac{1}{4000}$ of an inch (6 $\mu$). In the gravid uterus they undergo remarkable hypertrophy, measuring here $\frac{1}{80}$ to $\frac{1}{50}$ of an inch (300 to 500 $\mu$) in length, and $\frac{1}{2000}$ of an inch (12 $\mu$) in breadth.

In the contractile sheets formed of involuntary muscular tissue, the fibres are arranged side by side, are closely adherent, and their extremities are, as

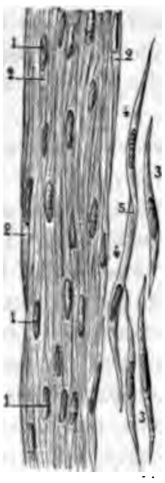

FIG. 147.—*Muscular fibres from the urinary bladder of the human subject; magnified 200 diameters* (Sappey).
1, 1, 1, nuclei; 2, 2, 2, borders of some of the fibres: 3, 3, isolated fibres; 4, 4, two fibres joined together at 5.

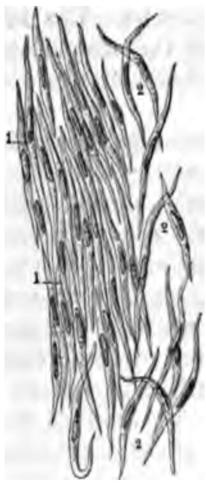

FIG. 148.—*Muscular fibres from the aorta of the calf; magnified 200 diameters* (Sappey).
1, 1, fibres joined with each other; 2, 2, 2, isolated fibres.

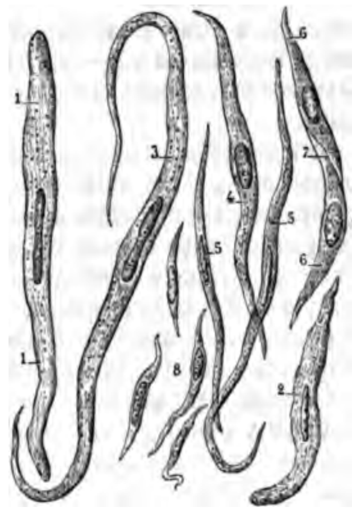

FIG. 149.—*Muscular fibres from the uterus of a woman who died at the ninth month of utero-gestation; magnified 350 diameters* (Sappey).
1, 1, 2, short, wide fibres; 3, 4, 5, 5, longer and narrower fibres; 6, 6, two fibres united at 7; 8, small fibres in process of development.

it were, dove-tailed into each other. Generally the borders of the fibres are regular and their extremities are simple; but sometimes the ends are forked and the borders present one or more little projections. The fibres seldom exist in a single layer except in the very smallest arterioles. Usually the layers are multiple, being superimposed in regular order. The action of acetic acid is to render the fibres pale so that their outlines become almost indistinguishable, and to bring the nuclei more distinctly into view.

*Contraction of the Involuntary Muscular Tissue.*—The mode of contraction of the involuntary muscles is peculiar. It does not take place immediately upon the reception of a stimulus, applied either directly or through the nerves, but it is gradual, enduring for a time and then followed by slow and gradual relaxation. A description of the peristaltic movements of the intestines gives an idea of the mode of contraction of these fibres, with the gradual propagation of the stimulus along the alimentary canal as the food makes its impression upon the mucous membrane. Another illustration is afforded by labor-pains. These are due to the muscular contractions of the uterus, and they last for a few seconds or one or two minutes. Their gradual access, continuation for a certain period, and gradual disappearance coincide with the history of the contractions of the involuntary muscular fibres.

The contraction of the involuntary muscular tissue is slow, and the fibres return slowly to a condition of repose. The movements are always involuntary. Peristaltic action is the rule, and the contraction takes place progressively and without oscillations. Contractility persists for a long time after death. Excitation of the nerves has less influence upon contraction of these fibres than direct excitation of the muscles. The involuntary muscular tissue is regenerated very rapidly, while the structure of the voluntary muscles is restored with great difficulty after destruction or division (Legros and Onimus).

*Physiological Anatomy of the Voluntary Muscular Tissue.*—A voluntary muscle contains, in addition to its peculiar contractile substance, fibres of inelastic and elastic tissue, adipose tissue, abundant blood-vessels, nerves and lymphatics, with certain nuclear and cellular anatomical elements. The muscular system in a well proportioned man is equal to about two-fifths of the weight of the body (Sappey). Its nutrition consumes a large proportion of the reparative material of the blood, while its disassimilation furnishes a corresponding quantity of excrementitious matter. The condition of the muscular system, indeed, is an almost unfailing evidence of the general state of the body, allowing, of course, for peculiarities in different individuals. Among the characteristic properties of the muscles, are elasticity, a constant and insensible tendency to contraction, called tonicity, the power of contracting forcibly on the reception of a proper stimulus, and a peculiar kind of sensibility. The relations of particular muscles, as taught by descriptive anatomy, involve special acts; but the most important physiological points connected with this system relate to the general properties and uses of the muscles.

The voluntary muscles are made up of a great number of microscopic fibres, known as the primitive muscular fasciculi. These are called red, striated or voluntary fibres. Their structure is complex, and they may be subdivided longitudinally into fibrillæ and transversely into disks. In very short muscles, some of the primitive fasciculi may run the entire length of the muscle; but the fasciculi usually are 1·2 to 1·6 inch (30 to 40 mm.) in length. The fasciculi, however, do not inosculate with each other, but the end of one fasciculus is united longitudinally with the end of another by a strongly adhesive substance, the line of union being oblique; so that the fibres practically run the entire length of the muscle. Each fasciculus is enclosed in its own sheath, without branching or inosculation. This sheath contains the true muscular substance only, and it is not penetrated by blood-vessels, nerves or lymphatics. In a thin, transverse section of a muscle, the divided ends of the fibres present an irregularly polygonal form with rounded corners. They seem to be cylindrical, however, when viewed in their length and isolated. Their color by transmitted light is a delicate amber, resembling the color of the blood-corpuscles.

The primitive fasciculi vary very much in size in different individuals, in the same individual under different conditions, and in different muscles. As a rule they are smaller in young persons and in females than in adult males. They are comparatively small in persons of slight muscular development. In persons of great muscular vigor, or when the general muscular system or particular muscles have been increased in size and power by exercise, the fasciculi are relatively larger. It is probable that the physiological increase in the size of a muscle from exercise is due to an increase in the size of the pre-

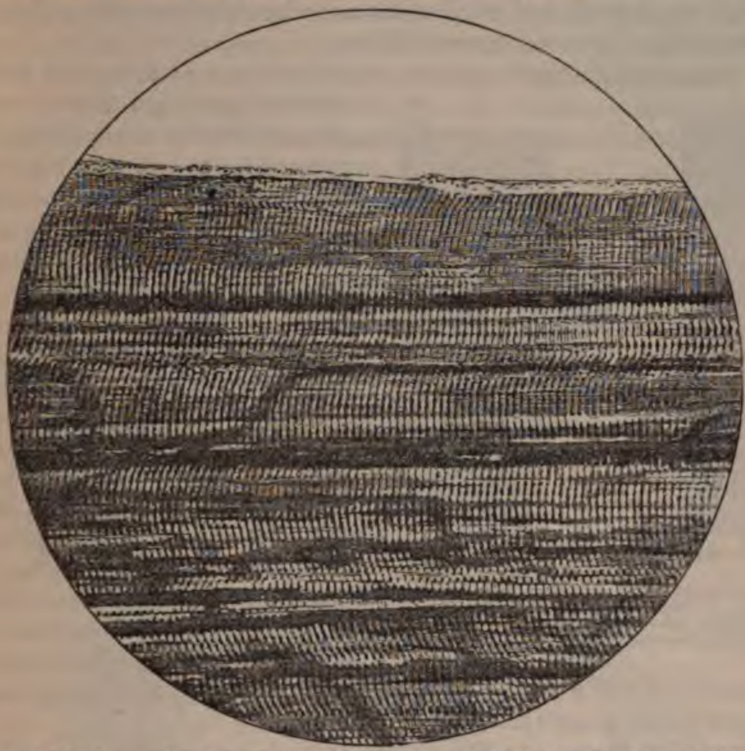

FIG. 150.—*Striated muscular fibres from the mouse; magnified 500 diameters* (from a photograph taken at the United States Army Medical Museum).
The injected capillaries are seen, somewhat out of focus.

existing fasciculi and not to the formation of new elements. In young persons the fasciculi are $\frac{1}{1700}$ to $\frac{1}{1200}$ of an inch (15 to 20 $\mu$) in diameter. In the adult they measure $\frac{1}{450}$ to $\frac{1}{250}$ of an inch (55 to 100 $\mu$).

The appearance of the primitive muscular fasciculi under the microscope is characteristic. They present regular, transverse striæ, formed of alternating dark and clear bands about $\frac{1}{25000}$ of an inch (1 $\mu$) wide. With a high magnifying power, a very fine transverse line is observed running through the middle of each one of the clear bands. In addition they present longitudinal striæ, not so distinct, and difficult to follow to any extent in the length of the fasciculus, but tolerably well marked, particularly in muscles that are habitually exercised. The muscular substance, presenting this peculiar, striated appearance, is enclosed in a very thin but elastic and resisting tubular membrane, called the sarcolemma or myolemma. This envelope can not be seen in ordinary preparations of the muscular tissue; but it frequently happens that the contractile muscular substance is broken, leaving the sarcolemma intact, which gives a good view of the membrane and conveys an idea of its strength and elasticity. Attached to the inner surface of the sarcolemma, are small, elongated nuclei with their long diameter in the direction of the fasciculi. These are usually not well seen in the unaltered muscle, but the addition of acetic acid renders the muscular substance pale and destroys the striæ, when the nuclei become distinct.

Water after a time acts upon the muscular tissue, rendering the fasciculi somewhat paler and larger. Acetic acid and alkaline solutions efface the striæ, and the fibres become semi-transparent. In fasciculi that are slightly decomposed, there is frequently a separation at the extremity into smaller fibres, called fibrillæ. These, when isolated, present the same striated appearance as the primitive fasciculus; viz., alternate dark and light portions. They measure about $\frac{1}{25000}$ of an inch (1 $\mu$) in diameter, and their number, in the largest primitive fibres, is estimated at about two thousand (Kölliker). The interior of each primitive fasciculus is penetrated by a very delicate membrane closely surrounding the fibrillæ. This arrangement may be distinctly seen in a thin section of a fibre treated with a solution of common salt in water, in the proportion of five parts per thousand (Kölliker).

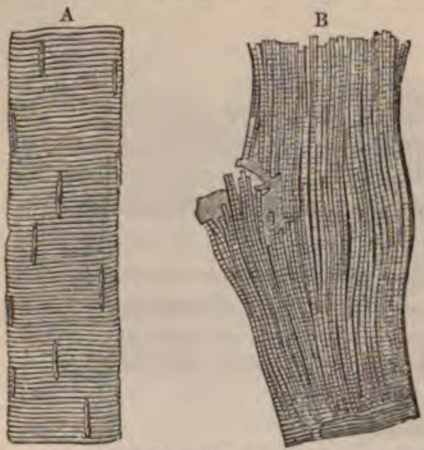


FIG. 151.—*Striated muscular fibres; magnified 250 diameters* (Sappey).

A, transverse striæ and nuclei of a primitive fasciculus; B, longitudinal striæ and fibrillæ of a primitive fasciculus in which the sarcolemma has been lacerated at one point by pressure.

*Connective Tissue.*—In the muscles there is a membrane surrounding a number of the primitive fasciculi. This is called the perimysium. The fibrous membranes that connect together the sesecondary bundles, with their contents, are enclosed in a sheath enveloping the whole muscle, sometimes called the external perimysium. The peculiarity of these membranes as distinguished from the sarcolemma is that they have a fibrous structure and are connected together throughout the muscle, while the tubes forming the sarcolemma are structureless and each one is distinct.

FIG. 152.—*Fibres of tendon of the human subject* (Rollett).

The name now most generally adopted for the ordinary fibrous tissue is connective tissue. It has been called cellular, areolar or fibrous, but most of these names were given to it without a clear idea of its structure. Its principal anatomical element is a fibre of excessive tenuity, wavy and with a single contour. These fibres are collected into bundles of variable size and are held together by an adhesive amorphous substance. The wavy lines that mark the bundles of fibres give them a very characteristic appearance.

The direction and arrangement of the fibres in the various tissues present marked differences. In the loose areolar tissue beneath the skin and between the muscles, and in the loose structure surrounding some of the glands and connecting the sheaths of blood-vessels and nerves to the adjacent parts, the bundles of fibres form a large net-work and are very wavy in their course. In the strong, dense membranes, as the aponeuroses, the proper coats of many glands, the periosteum and perichondrium and the serous membranes, the waves of the fibres are shorter, and the fibres themselves interlace much more closely. In the ligaments and tendons, the fibres are more nearly straight and are arranged longitudinally.

On the addition of acetic acid the bundles of inelastic fibres swell up, become semi-transparent, and the nuclei and elastic fibres are brought into

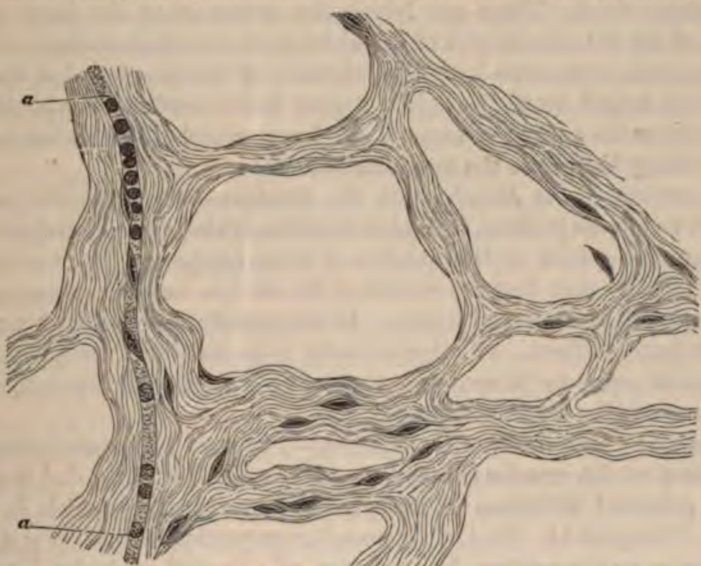


FIG. 153.—*Loose net-work of connective tissue from the human subject, showing the fibres and cells* (Rollett).
*a*, *a*, a capillary blood-vessel.

view. The proportion of elastic fibres differs very much in different situations, but they are all of the smallest variety, and they present a striking contrast to the inelastic fibres in their form and size. Although they are very small, they always present a double contour.

Certain cellular and nuclear elements are always found in the connective tissue. The cells are known as connective-tissue cells. They are very irregular in size and form, some of them being spindle-shaped or caudate, and of its strength and elasticity. Attached to the inner surface of the sarcolemma, are small, elongated nuclei with their long diameter in the direction of the fasciculi. These are usually not well seen in the unaltered muscle, but the addition of acetic acid renders the muscular substance pale and destroys the striæ, when the nuclei become distinct.

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A B

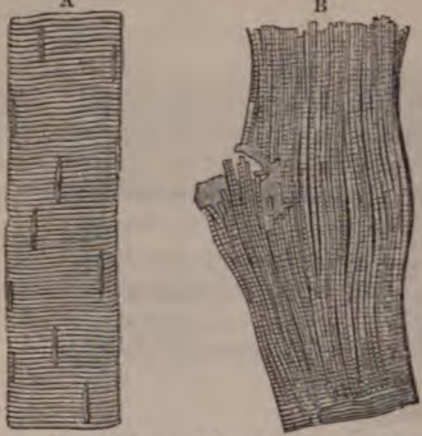

FIG. 151.—*Striated muscular fibres; magnified 250 diameters* (Sappey).
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FIG. 152.—*Fibres of tendon of the human subject* (Rollett).

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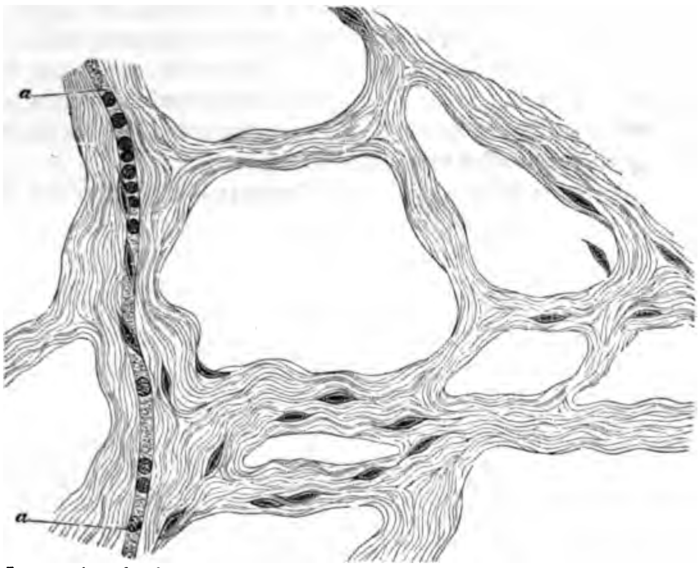



FIG. 158.—*Loose net-work of connective tissue from the human subject, showing the fibres and cells* (Rollett).
*a, a,* a capillary blood-vessel.

view. The proportion of elastic fibres differs very much in different situations, but they are all of the smallest variety, and they present a striking contrast to the inelastic fibres in their form and size. Although they are very small, they always present a double contour.

Certain cellular and nuclear elements are always found in the connective tissue. The cells are known as connective-tissue cells. They are very irregular in size and form, some of them being spindle-shaped or caudate, and others, star-shaped. They possess one, and sometimes two or three clear, ovoid nuclei, with distinct nucleoli. On the addition of acetic acid the cells disappear but the nuclei are unaffected. It is impossible to give any accurate measurements of the cells, on account of their great variations in size. The appearance of the connective tissue, with a few cells and nuclei, is represented in Fig. 153.

Between the muscles, and in the substance of the muscles, between the bundles of fibres, there always exists a greater or less quantity of adipose tissue in the meshes of the fibrous structure.

*Blood-vessels and Lymphatics.*—The muscles are abundantly supplied with blood-vessels, generally by a number of small arteries with two satellite veins. The capillary arrangement in this tissue is peculiar. From the smallest arterioles, capillary vessels are given off, arranged in a net-work with tolerably regular, oblong, rectangular meshes, their long diameter following the direction of the fibres. These envelop each primitive fasciculus, enclosing it completely, the artery and vein being upon the same side. The capillaries are smaller than in any other part of the vascular system.

The arrangement of the lymphatics in the muscles has never been definitely ascertained. There are lymphatics surrounding the large vascular trunks of the extremities and of the abdominal and thoracic walls, which, it would appear, must come from the substance of the muscles; but they have never been traced to their origin. Sappey has succeeded in injecting lymphatics upon the surface of some of the larger muscles, but he has not been able to follow them into the muscular substance.

*Connection of the Muscles with the Tendons.*—The primitive muscular fasciculi terminate in little, conical extremities, which are received into corresponding depressions in the bundles of fibres composing the tendons; but this union is so close that the muscle or the tendon may be ruptured without a separation at the point of union. In the penniform muscles this arrangement is quite uniform. In other muscles it is essentially the same, but the perimysium seems to be continuous with the loose areolar tissue enveloping the corresponding tendinous bundles.

*Chemical Composition of the Muscles.*—The most important nitrogenized constituent of the muscles is myosine. This resembles fibrin, but it presents certain points of difference in its behavior to reagents, by which it may be readily distinguished. One of its peculiar properties is that it is dissolved at an ordinary temperature by a mixture of one part of hydrochloric acid and ten of water. The muscular substance is permeated by a fluid, called the muscular juice, which contains certain coagulable albuminoid substances. Combined with the organic constituents of the muscular substance are mineral salts in great variety, which can not be separated without incineration. Certain excrementitious matters have also been found in the muscles; and probably nearly all of those eliminated by the kidneys exist here, although they are taken up by the blood as fast as they are produced and are consequently detected with difficulty. The muscles also contain inosite, inosic acid, lactic acid and certain volatile acids of fatty origin. During life the muscular fluid is slightly alkaline, but it becomes acid soon after death. The muscle itself, during contraction, has an acid reaction. The muscular juice is alkaline or neutral after moderate exercise as well as during complete repose; but when a muscle is made to undergo excessive exercise, the lactic and other acids exist in greater quantity and the reaction becomes acid.

## Physiological Properties of the Muscles.

The important general properties of the striated muscles are the following: 1. Elasticity; 2. Tonicity; 3. Sensibility of a peculiar kind; 4. Contractility, or excitability. These are all necessary to the physiological action of the muscles. Their elasticity is brought into play in opposing muscles or sets of muscles; one set acting to move a part and to extend the antagonistic muscles, which, by virtue of their elasticity, retract when the extending force is removed. Their tonicity is an insensible and a more or less constant contraction, by which the action of opposing muscles is balanced when both are in the condition of what is called repose. Their sensibility is peculiar and is expressed chiefly in the sense of fatigue and in the appreciation of weight and of resistance to contraction. Their contractility or excitability is the property which enables them to contract under stimulation. All of these general properties strictly belong to physiology, as do some special acts that are not necessarily involved in the study of ordinary descriptive anatomy.

*Elasticity of Muscles.*—The true muscular substance contained in the sarcolemma is eminently contractile; and although it may possess a certain degree of elasticity, this property is most strongly marked in the accessory anatomical elements. The interstitial fibrous tissue is loose and presents a certain number of elastic fibres; and the sarcolemma is very elastic. It is probably the sarcolemma that gives to the muscles their retractile power after simple extension.

It is unnecessary to follow out in detail all of the many experiments that have been made upon the elasticity of muscles. There is a certain limit, of course, to their perfect elasticity—understanding by this the degree of extension that is followed by complete retraction—and this can not be exceeded in the human subject without dislocation of parts. It has been found by Marey, that the gastrocnemius muscle of a frog, detached from the body, can be extended about $\frac{1}{50}$ of an inch (0·5 mm.) by a weight of a little more than 300 grains (20 grammes). This weight, however, did not extend the muscle beyond the limit of perfect elasticity. The muscle of a frog of ordinary size was extended beyond the possibility of complete restoration, by a weight of about seven hundred and fifty grains (48·6 grammes). Marey also showed that fatigue of the muscles increased their extensibility and diminished their power of subsequent retraction. This fact has an application to the physiological action of muscles; for it is well known that they are unusually relaxed during fatigue after excessive exertion, and they are at that time more than ordinarily extensible.

*Muscular Tonicity.*—The muscles, under normal conditions, have an insensible and a constant tendency to contract, which is more or less dependent upon the action of the motor nerves. If, for example, a muscle be cut across in a surgical operation, the divided extremities become permanently retracted; or if the muscles of one side of the face be paralyzed, the muscles upon the opposite side insensibly distort the features. It is difficult to explain these phenomena by assuming that tonicity is due to reflex action, for there is no evidence that the contraction takes place as the consequence of a stimulus. All that can be said is that a muscle, not excessively fatigued, and with its nervous connections intact, is constantly in a state of insensible contraction, more or less marked.

*Sensibility of the Muscles.*—The muscles possess that kind of sensibility which gives an appreciation of the power of resistance, immobility, and elasticity of substances that are grasped, or which, by their weight, are opposed to the exertion of muscular power. It is by the appreciation of weight and resistance that the force required to accomplish muscular acts is regulated. These properties refer chiefly to simple muscular efforts. After long-continued exertion there is a sense of fatigue that is peculiar to the muscles. It is difficult to separate this entirely from the sense of nervous exhaustion, but it seems to be to a certain extent distinct; for when suffering from the fatigue that follows over-exertion, it seems as though a nervous stimulus could be sent to the muscles, to which they are for the time unable to respond.

When the muscles are thrown into tetanic contraction, a peculiar sensation is produced, which is entirely different from painful impressions made upon the ordinary sensory nerves. In the cramps of cholera, tetanus, or the convulsions from strychnine, these distressing sensations are very marked.

If the muscles possess any general sensibility, it is very slight. A muscle may be lacerated or irritated without producing actual pain, although contraction produced by irritants and the sense of tension when the muscles are drawn upon can always be appreciated.

*Muscular Contractility, or Excitability.*—During life and under normal conditions, the muscles will always contract in obedience to a proper stimulus applied either directly or through the nerves. In the natural action of the organism, this contraction is induced by nervous influence either through volition or reflex action. Still, a muscle may be living and yet have lost its contractility. For example, after a muscle has been for a long time paralyzed and disused, the application of the most powerful stimulus will fail to induce contraction; but when examined with the microscope, it is found that the nutrition of the muscle has become profoundly affected, and that the contractile substance has disappeared. Muscular contractility persists for a certain time after death and in muscles separated from the body; and this fact has been taken advantage of by physiologists in the study of the properties of the muscular tissue. A muscle detached from the living body continues for a time to respire, and it undergoes some of the changes of disassimilation observed in the organism. So long as these changes are restricted within the limits of physical and chemical integrity of the fibre, contractility remains. As these processes are very slow in the cold-blooded animals, the excitability of all the parts persists for a considerable time after death.

In the human subject and the warm-blooded animals, the muscles cease to respond to a stimulus a few hours after death, although the time of disappearance of excitability is very variable. Nysten, in a number of experiments upon the disappearance of excitability in the human subject after decapitation, found that different parts lost their contractility at different periods, but that generally this depended upon exposure to the air. With the exception of the right auricle of the heart, the striated muscles were the last to lose their excitability. In one instance, certain of the voluntary muscles that had not been exposed retained their contractility seven hours and fifty minutes after death. Longet and Masson found that an electric shock, sufficiently powerful to produce death instantly, destroyed the excitability of the muscular tissue and of the motor nerves.

The experiments of Longet (1841) presented almost conclusive proof of the independence of muscular excitability. He resected the facial nerve and found that it ceased to respond to mechanical and electric stimulus, or in other words, lost its excitability, after the fourth day. Operating, however, upon the muscles supplied exclusively with filaments from this nerve, he found that they responded promptly to mechanical and electric stimulation, and that this continued for more than twelve weeks. In other experiments it was shown that while the contractility of the muscles could be seriously influenced through the nervous system, this was effected only by modifications in their nutrition. When the mixed nerves were divided, the nutrition of the muscles was generally disturbed; and although muscular contractility persisted for some time after the nervous excitability had disappeared, it became very much diminished at the end of six weeks. Some varieties of curare destroy the excitability of the motor nerves, leaving the sensitory filaments intact. If a frog be poisoned by introducing a little of this agent under the skin, stimulation, electric or mechanical, applied to an exposed nerve, fails to produce muscular contraction; but if the stimulus be applied directly to the muscles, they will contract vigorously. In this way the nerves are, as it were, dissected out from the muscles; and the discovery of an agent that will paralyze the nerves without affecting the muscles affords conclusive proof that the excitability of these two systems is distinct. If a frog be poisoned with potassium sulphocyanide, precisely the contrary effect is observed; that is, the muscles will become insensible to excitation, while the nervous system is unaffected. This fact may be demonstrated by apply-

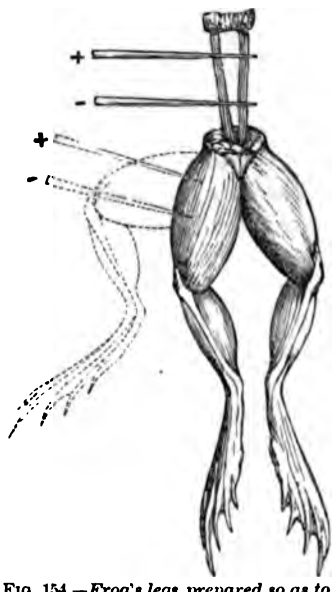


FIG. 154.—*Frog's legs prepared so as to show the effects of curare* (Bernard). Faradization of the nerves in this animal, which has been poisoned with curare, has no effect; while the stimulus applied directly to the muscles (see dotted lines) produces contraction.

ing a tight ligature around the body in the lumbar region, involving all the parts except the lumbar nerves. If the poison be now introduced beneath the skin above the ligature, only the anterior parts are affected, because the vascular communication with the posterior extremities is cut off. If the exposed nerves be now stimulated, the muscles of the legs are thrown into contraction, showing that the nervous excitability remains. Reflex movements in the posterior extremities may also be produced by irritation of the parts above the ligature. These experiments leave no doubt of the existence of an inherent and independent excitability in the muscular tissue (Bernard). Contractions of muscles, it is true, are normally excited through the nervous system, and artificial stimulation of a motor nerve is the most efficient method of producing the simultaneous action of all the fibres of a muscle or of a set of muscles; but electric, mechanical, or chemical irritation of the muscles themselves will produce contraction, after the nervous excitability has been abolished. The conditions under which muscular contractility exists are simply those of normal nutrition of the muscular tissue. When the muscles have become profoundly affected in their nutrition, as the result of section of the mixed nerves or after prolonged paralysis, their excitability disappears and can not be restored.

Experiments have been made with regard to the influence of the circulation upon muscular excitability, chiefly with reference to the effects of tying large vessels. Longet tied the abdominal aorta in five dogs and found that voluntary motion ceased in about a quarter of an hour, and that the muscular excitability was extinct in two hours and a quarter. When the circulation was restored, after three or four hours, by removing the ligature, the excitability, and finally voluntary movement, returned. These experiments show that the circulation of the blood is necessary to the contractility of the muscles. Tying the vena cava did not affect the excitability of the muscles. In dogs in which this experiment was performed, the lower extremities preserved their contractility, and the voluntary movements were unaffected up to the time of death, which took place in twenty-six hours.

The relations of muscular excitability to the circulation have been farther illustrated in the following experiments by Brown-Séquard: The first observations were made upon two men executed by decapitation. Thirteen hours and ten minutes after death, when the muscular excitability had disappeared and was succeeded by cadaveric rigidity, a quantity of fresh, defibrinated venous blood from the human subject was injected into the arteries of one hand and was returned by the veins. It was afterward re-injected several times during a period of thirty-five minutes. The whole time occupied in the different injections was ten to fifteen minutes. Ten minutes after the last injection, and about fourteen hours after death, the excitability was found to have returned in a marked degree in twelve muscles of the hand. There were only two muscles out of the nineteen, in which the excitability could not be demonstrated. Three hours after, the excitability still existed, but it disappeared a quarter of an hour later. The second observation was essentially the same, except that defibrinated blood from the dog was used and the experiments were made upon the muscles of the arm. The excitability was restored in all of the muscles, and it persisted, the cadaveric rigidity having disappeared, twenty hours after decapitation.

## MUSCULAR CONTRACTION.

The stimulus of the will, conveyed through the conductors of motor impulses from the brain to a muscle or set of muscles, excites the muscular fibres and causes them to contract. In muscles that have been exercised and educated, this action is regulated with great nicety, so that the most delicate and rapid as well as powerful contractions may be produced. Certain movements, not under the control of the will, are produced as the result of unconscious reflection from a nervous centre, along the motor conductors, of an impression made upon sensory nerves. During this action certain important phenomena are observed in the muscles themselves. They change in form, consistence, and to a certain extent, in their constitution; the different periods of their stimulation, contraction and relaxation are positive and well marked; their nutrition is for the time modified; they develop galvanic currents; and in short, they present a number of general phenomena, distinct from the results of their action, that are more or less important.

The most prominent of the phenomena accompanying muscular action is shortening and hardening of the fibres. It is necessary only to observe the action of any well developed muscle to appreciate these changes. The active shortening is shown by the approximation of the points of attachment, and the hardening is sufficiently palpable. The latter phenomenon is marked in proportion to the development of the true muscular tissue and its freedom from inert matter, such as fat. It is the muscular substance alone which has the property of contraction; and this action increases the consumption of oxygen and probably of other matters, the formation of carbon dioxide and some other excrementitious products, and develops heat.

Notwithstanding the marked and constant changes in the form and consistence of the muscles during contraction, their actual volume undergoes modifications so slight that they may practically be disregarded. The exceeding slight change which has been observed in recent experiments (Valentin, Landois) is a diminution in volume.

*Changes in the Form of the Muscular Fibres during Contraction.*—All physiologists are agreed that in muscular contraction there is an increase in the thickness of the fibre, nearly compensating its diminution in length. This has been repeatedly observed in microscopical examinations, and the only points now to determine are the exact mechanism of this transverse enlargement, its duration, the means by which it may be excited, and its physiological modifications. These questions have been made the subjects of investigation by Helmholtz, Du Bois-Reymond, Aeby, Marey and others; and although it is hardly necessary to follow these experimenters through all the details of their observations, many important points have been developed, particularly by the methods of registering the muscular movements.

One essential condition in the study of the mechanism of muscular contraction is to imitate, in a muscle or a part of a muscle that can be subjected to direct observation, the force that naturally excites it to contraction. The application of electricity to the nerve is the most perfect method that can be employed for this purpose. In this way a single contraction may be produced, or by employing a rapid succession of impulses, so-called tetanic action may be excited. While the electric current is not identical with the nervous force, it is the best substitute that can be used in experiments upon muscular contractility, and it has the advantage of affecting but little the physical and chemical integrity of the nervous and muscular tissues.

There are two classes of phenomena that may be produced by electric excitation of motor nerves: 1. When the stimulus is applied in the form of a single discharge, it is followed by a single muscular contraction. 2. Under a rapid succession of discharges, the muscle is thrown into a state of permanent, or tetanic contraction. It will facilitate a comprehension of the subject to study these phenomena separately and successively.

*Mechanism of a Single Muscular Contraction.*—If an electric discharge, even very feeble, be applied to a motor nerve connected with a fresh muscle, it is followed by a sudden contraction, which is succeeded by a rapid relaxation. Under this stimulation, the muscle shortens by about three-tenths of its entire length. The form of the contraction, as registered by the apparatus of Helmholtz, Marey and others who have applied the graphic method to the study of muscular action, presents certain peculiarities.

According to Helmholtz, the whole period of a single contraction and relaxation of the gastrocnemius muscle of a frog is a little less than one-third of a second. The muscles of mammals and birds contract more rapidly, but with this exception, the essential characters of the contraction are the same. The following are the periods occupied by these different phenomena in the gastrocnemius of a frog:

| | |
|---|---|
| Interval between stimulation and contraction (latent period) | 0"·020 |
| Contraction | 0"·180 |
| Relaxation | 0"·105 |
| | 0"·305 |

The latent period in man is 0·004 to 0·01 of a second, the contraction occupies 0·03 to 0·4 of a second, and the period of relaxation is a little shorter than the period of contraction. The duration of the electric current is only 0"·0008. This description represents the contraction of an entire muscle, but it does not indicate the changes in form of the individual fibres, a point much more difficult to determine satisfactorily. It is well established, however, that a single fibre, with its excitability unimpaired, becomes contracted and swollen at the point where the stimulation is applied. The question now is whether, in normal contraction of the fibres in obedience to the natural nervous stimulus, there be a uniform shortening of the whole fibre, a shortening of those portions only that are the seat of the terminations of the motor nerves, or a peristaltic shortening and swelling, rapidly running the length of the fibre.

The experiments of Aeby, which have been repeated and extended by Marey, have shown that when one extremity of a muscle is excited, a contraction occurs at that point and is propagated along the muscle, in the form of a wave. The estimated rapidity of this wave is 33 to 43 feet (10 to 13 metres) per second (Hermann). Applying this principle to the physiological action of muscles, Aeby proposed the theory that shortening of the fibres takes place wherever a stimulus is received, and that this is propagated in the form of a wave, which meets in its course another wave starting from a different point of stimulation. Although this view of the physiological action of the muscular fibres is very probable, it can not be assumed that it has been absolutely demonstrated; but it is certainly more satisfactory and better sustained by experimental facts than any other theory that has yet been advanced.

*Mechanism of Tetanic Muscular Contraction.*—By a voluntary effort a muscular contraction may be produced, of a certain duration and of a power, within certain limits, proportionate to the amount of force required; but after a time the muscle becomes fatigued, and it may become exhausted to the extent that it will no longer respond to the normal stimulus. This normal muscular action in obedience to impulses conveyed by motor nerves may be closely imitated by electric stimulation. When a single electric discharge is applied to a nerve, there is a single muscular contraction; but a rapid succession of discharges produces a persistent contraction, which is called tetanic.

During the passage of a feeble galvanic current through a nerve, there is no contraction in the muscles to which the nerve is attached; and it is only when the circuit is closed or opened that any action is observed. The interrupted galvanic current, the induced current, or a succession of discharges of statical electricity, when they do not follow each other too rapidly, produces a corresponding succession of muscular contractions. As the rapidity of these electric impulses is increased, the individual contractions become less and less distinct, until finally the contraction is persistent. Distinct single contractions occur with ten excitations per second, a partial fusion of the different acts takes place with twenty per second, and a complete fusion, or tetanus, with twenty-seven per second (Marey). When the contraction becomes continuous, there is an elevation of the line marked on a registering apparatus, showing increased power as the excitations are more and more rapid. This is artificial tetanus; but it probably is the kind of contraction that occurs in the physiological action of the voluntary muscles.

It is probable that the normal nervous stimulus in voluntary muscular action is a succession of impulses, which produce a power of muscular contraction that is proportionate to their rapidity. Vibrations, which are more or less regular, actually occur during the contraction of muscles (Wollaston, Haughton, Helmholtz). Helmholtz, indeed, has recognized a musical note produced by contracting muscles, which exactly corresponds to the number of excitations per second applied to the nerve. This can be heard in the temporal and masseter muscles by filling the ears with wax and causing these muscles to contract. The number of vibrations noted by Helmholtz was 19½ per second; but the sound heard was the first overtone, or the octave, the fundamental tone being too low to be appreciated by the ear.

Some physiologists have denied the supposed identity between the tetanic contraction produced by a rapid succession of stimuli applied to a motor nerve and voluntary muscular contraction. Complete fusion of contraction occurs with twenty-seven or more stimuli per second applied to a nerve; but it is stated that stimuli applied to the motor cerebral centres, even when very rapid, do not produce more than eight to thirteen muscular contractions, the average being ten per second (Horsley and Schäfer, 1887). The average in voluntary muscular contraction is about the same. From these observations it is argued that the rate of so-called vibration in voluntary muscular contraction has an average of about ten per second. This conclusion is based upon actual myographic tracings. It is difficult, however, to reconcile these results with those obtained by Marey, Helmholtz and others. It is a fact, also, that distinct muscular contractions may be produced very rapidly by an effort of the will. It is not difficult for any one to make five taps of the finger per second for a few seconds, and skillful performers on musical instruments are able, by using the same muscle or set of muscles, to make movements that are very much more rapid, each movement presumably requiring a distinct nervous impulse. It may be that in an unweighted muscle, the contractions are discontinuous, and that the average number of waves is about ten per second; but it is probable that the estimate of Helmholtz—19½ waves per second—is nearly correct for muscles in a condition of powerful contraction. In a series of observations by Griffiths (1888), it was found that voluntary contraction of the biceps weighted with a little more than eleven pounds (5,000 grammes), for one hundred seconds, gave an average of eighteen waves per second, the average for the unweighted muscle being fourteen waves per second for thirty-three seconds.

The nerves are not capable of conducting an artificial stimulus for an indefinite period, nor are the muscles able to contract for more than a limited time upon the reception of such an excitation. The electric current may be made to destroy for a time both the nervous and muscular excitability; and these properties become gradually extinguished, the parts becoming fatigued before they are completely exhausted. Precisely the same phenomena are observed in the physiological action of muscles. When a muscle is fatigued artificially, a tetanic condition is excited more and more easily, but the power of the contraction is proportionally diminished. Muscles contracting in obedience to an effort of the will pass through the same stages of action. It is probable that constant contraction is excited more and more easily as the muscles become fatigued, because the nervous force gradually diminishes in intensity; but it is certain that the vigor of contraction at the same time progressively diminishes.

The phenomena of muscular contraction thus far considered are those produced by voluntary effort or by stimulation of motor nerves; but many important phenomena have been observed in muscles detached from the body and stimulated directly. These observations have generally been made on the gastrocnemius of the frog, the phenomena being recorded by a registering apparatus, the simplest form of which is the myograph of Helmholtz. This instrument is used in recording muscular contractions by causing the recording point to play upon a smoked paper moving at a known rate. If the muscle of the frog, slightly weighted, be stimulated by a single induction-shock, there is first a latent period, when there is no contraction, then a contraction followed by relaxation, and finally a slight, elastic vibration before the muscle becomes quiescent. These phenomena are illustrated in the curve given in Fig. 156 in which, however, the latent period is not measured.

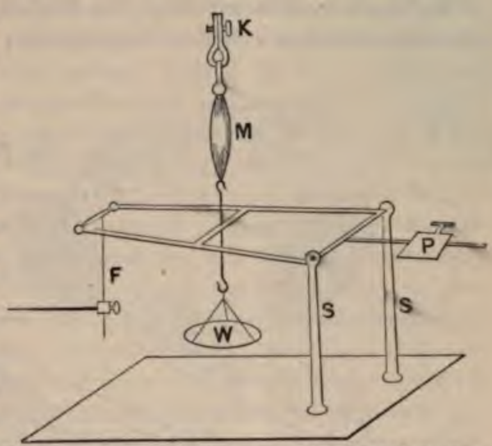



Fig. 155.—*Diagram of the myograph of Helmholtz* (Landois).

M, muscle fixed by the clamp (K) by a portion of the femur; F, recording point; P, counterpoise used to balance the lever; W, pan for weights; S, S, supports for the lever.

In a muscle prepared in this way, the maximum of stimulation and the maximum of power measured by a weight lifted can readily be ascertained, and certain phenomena due to fatigue of the muscle have been observed. In a fatigued muscle, the latent period is lengthened and the elevation of the curve of contraction is not so high, showing a slower and longer action. When a muscle is excited to tetanic contraction by a rapidly interrupted current of considerable strength, the elevation produced by the initial contraction is nearly vertical, and is followed by a horizontal straight line which marks the tetanic condition. The phenomena induced by direct stimulation of muscles are somewhat exaggerated when the stimulus is applied to the motor nerve.


Fig. 156.—*Curve of a single muscular contraction* (Landois).

A F, abscissa; A C, ordinate; A B, latent period; B D, period of contraction; D E, period of relaxation; E F, elastic vibration.

*Electric Phenoména in Muscles.*—It was ascertained a number of years ago, by Matteucci, that all living muscles present electric currents. The direction of these currents is from the longitudinal surface to the transverse, or cut surface of the muscle, as is shown in Fig. 157. A simple method of demonstrating the muscular current is to prepare the leg of a frog with the crural nerve attached, and to apply one portion of the nerve to the deep parts of an incised muscle and the other to the surface. As soon as the connection is made, a contraction of the leg takes place. The current may also be demonstrated with an ordinary galvanometer; but the evidence obtained by the frog's leg is sufficiently conclusive.

Matteucci constructed out of the fresh muscles from the thigh of the frog, what is sometimes called a frog-battery; which is made by taking the muscles of the lower half of the thigh from several frogs, removing the bones, and arranging them in a series, each with its conical extremity inserted into the central cavity of the one below. In this way the external surface of each thigh except the last is in contact with the internal surface of the one below. If the two extremities of the pile be connected with a galvanometer, quite a powerful current from the internal to the external surface of the muscle may be demonstrated. In a pile formed of ten elements, the needle of a galvanometer was deviated 30° to 40°.

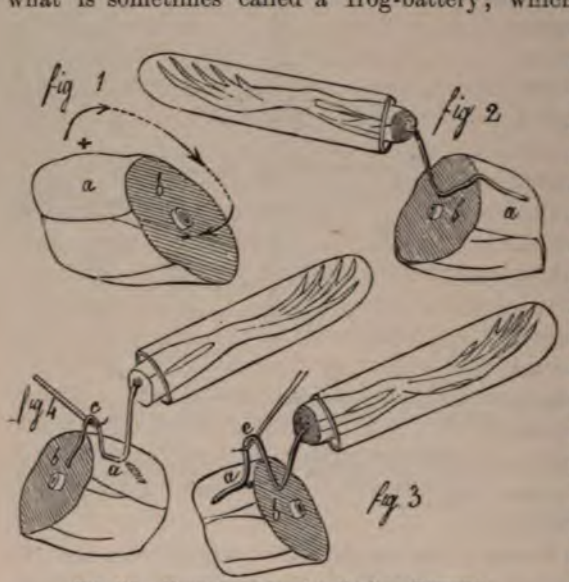



FIG. 157.—*Muscular current in the frog* (Bernard).

Fig. 1, portion of the thigh, with the skin removed; *a*, surface of the muscles; *b*, section; the direction of the current is indicated by the arrow.
Fig. 2, the nerve of a frog's leg (the leg enclosed in a glass tube) is applied to the section and the surface of the muscle. There is no contraction, because it is necessary that a portion of the nerve should be raised up.
Fig. 3, a portion of the nerve is raised with a glass rod. The contraction of the galvanoscopic leg occurs at the making of the circuit, because the current follows the course of the nerve, or is descending.
Fig. 4, the contraction here occurs at the breaking of the circuit, because the direction of the current is opposite the course of the nerve, or is ascending.

Electric currents are observed in all living muscles, but they are most marked in the mammalia and warm-blooded animals. They exist, also, for a certain time after death. Artificial tetanus of the muscles, however, instead of intensifying the current, causes the galvanometer to recede. If, for example, the needle of the instrument show a deviation of 30° during repose, when the muscle is excited to tetanic contraction, it will return so as to mark only 10° or 15°, or it may even return to zero. This phenomenon, which is called negative variation of the muscular current, is observed only during a continued muscular contraction and it does not attend a single contraction.

*Muscular Effort.*—The mere voluntary movement of parts of the body, when there is no obstacle to be overcome or no great force is required, is very different from a muscular effort. For example, in ordinary progression there is simply a movement produced by the action of the proper muscles, almost without consciousness, and this is unattended with any considerable modification in the circulation or respiration; but in attempting to lift a heavy weight, to jump, to strike a powerful blow or to make any vigorous effort, the action is different. In the latter instance, a certain preparation for the muscular effort is made by inflating the lungs, closing the glottis and contracting more or less forcibly the expiratory muscles so as to render the thorax rigid and unyielding; and by a concentrated effort of the will, the proper muscles are then brought into action. This action of the muscles of the thorax and abdomen, due to simple effort and independent of the particular muscular act that is to be accomplished, compresses the contents of the rectum and bladder and obstructs very materially the venous circulation in the large vessels. It is well known that hernia frequently is produced in this way; the veins of the face and neck become turgid; the conjunctiva may become ecchymosed; and sometimes aneurismal sacs are ruptured. An effort of this kind is generally of short duration, and it can not, indeed, be prolonged beyond the time during which respiration can be conveniently arrested.

There are degrees of effort which are not attended with this powerful action of the muscles of the chest and abdomen, and in which the glottis is not completely closed; and an opening into the trachea or larynx, rendering immobility of the thorax impossible, does not interfere with certain acts that require considerable muscular power. If the glottis be exposed in a dog, when he makes violent efforts to escape, the opening is firmly closed. This is often observed in vivisections; but Longet has shown that dogs with an opening into the trachea are frequently able to run and leap with "astonishing agility." He also saw a horse, with a large canula in the trachea, that performed severe labor and drew heavily loaded wagons in the streets of Paris.

## Passive Organs of Locomotion.

It would be out of place to describe fully and in detail all of the varied and complex movements produced by muscular action. Many of these, such as the movements of deglutition and of respiration, are necessarily considered in connection with the functions of which they form a part; but others are purely anatomical questions. Associated and antagonistic movements, automatic and reflex movements etc., belong to the history of the motor nerves and will be fully considered in connection with the physiology of the nervous system.

The study of locomotion involves a knowledge of the physiological anatomy of certain passive organs, such as the bones, cartilages and ligaments. Although a complete history of the structure of these parts trenches somewhat upon the domain of anatomy, a brief description of their histology will practically complete the account of the tissues of the body, with the exception of the nervous system and the organs of generation, which will be taken up hereafter.

Locomotion is effected by the muscles acting upon certain passive, movable parts. These are the bones, cartilages, ligaments, aponeuroses and tendons. The fibrous structures have already been described, and it only remains to study the structure of bones and cartilages.

*Physiological Anatomy of the Bones.*—The bones are composed of what is called the fundamental substance, with cavities and canals of peculiar form.

The cavities contain corpuscular bodies called bone-corpuscles. The canals of larger size serve for the passage of blood-vessels, while the smaller canals (canaliculi) connect the cavities with each other and finally with the vascular tubes. Many of the bones present a medullary cavity, filled with a peculiar structure called marrow. In almost all bones there are two distinct portions; one, which is exceedingly compact, and the other, more or less spongy or cancellated. The bones are also invested with a membrane, containing vessels and nerves, called the periosteum.

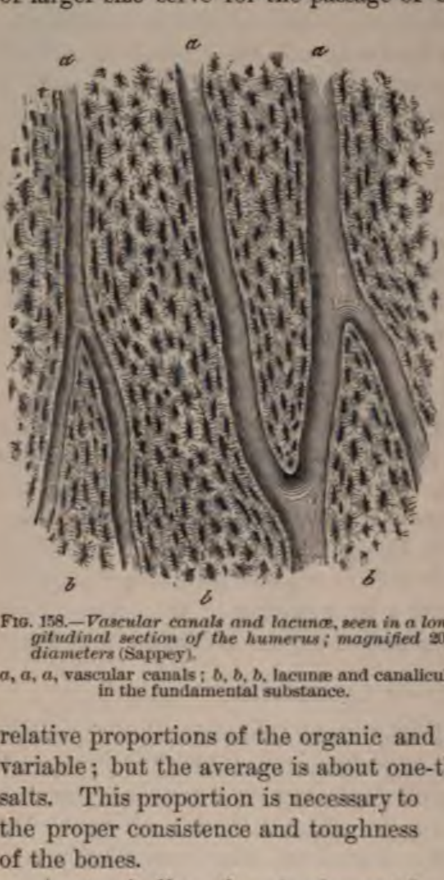



Fig. 158.—*Vascular canals and lacunæ, seen in a longitudinal section of the humerus; magnified 200 diameters* (Sappey).
*a, a, a*, vascular canals; *b, b, b*, lacunæ and canaliculi in the fundamental substance.

The fundamental substance is composed of an organic matter, called osseine, combined with various inorganic salts, in which calcium phosphate largely predominates. In addition to calcium phosphate, the bones contain calcium carbonate, calcium fluoride, magnesium phosphate, sodium phosphate and sodium chloride. The relative proportions of the organic and inorganic constituents are somewhat variable; but the average is about one-third of the former to two-thirds of salts. This proportion is necessary to the proper consistence and toughness of the bones.

Anatomically, the fundamental substance of the bones is arranged in the form of regular, concentric lamellæ, about $\frac{1}{3000}$ of an inch (8 $\mu$) in thickness. This matter is of an indefinitely and faintly striated appearance, but it can not be reduced to distinct fibres. In the long bones the arrangement of the lamellæ is quite regular, surrounding the Haversian canals and forming what are sometimes called the Haversian rods, following in their direction the length of the bone. In the short, thick bones the lamellæ are more irregular, frequently radiating from the central portion toward the periphery.

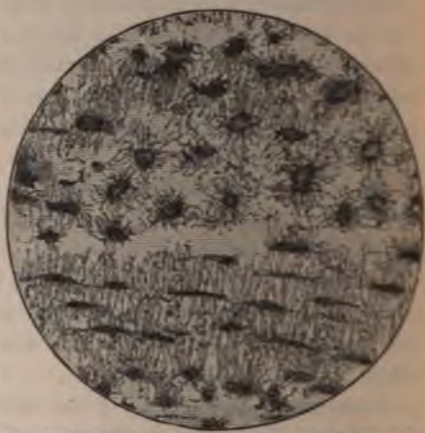


Fig. 159.—*Longitudinal section of bone, from the shaft of the human femur; magnified 180 diameters* (from a photograph taken at the United States Army Medical Museum).

The Haversian canals exist in the compact bony structure. They are either absent or are very few in the spongy and reticulated portions. Their form is rounded or ovoid, the larger canals being sometimes quite irregular. In the long bones their direction is generally longitudinal, although they anastomose by lateral branches. Each one of these canals contains a blood-vessel, and their disposition constitutes the vascular arrangement of the bones. They are all connected with the openings on the surface of the bones, by which the arteries penetrate and the veins emerge. Their size, of course, is variable. The largest are about $\frac{1}{60}$ of an inch (400 $\mu$) and the smallest, $\frac{1}{800}$ of an inch (30 $\mu$) in diameter (Sappey). Their average size is $\frac{1}{250}$ to $\frac{1}{200}$ of an inch (100 to 125 $\mu$). In a transverse section of a long bone, the Haversian canals may be seen cut across and surrounded by twelve to fifteen lamellæ.

*Lacunæ.*—The fundamental substance is everywhere marked by irregular, microscopic excavations, of a peculiar form, called lacunæ. They are connected with little canals, giving them a stellate appearance. These canals are most abundant at the sides of the lacunæ. The lacunæ measure $\frac{1}{1250}$ to $\frac{1}{800}$ of an inch (20 to 30 $\mu$) in their long diameter, by about $\frac{1}{2500}$ of an inch (10 $\mu$) in width.

*Canaliculi.*—These are little, wavy canals, connecting the lacunæ with each other and presenting a communication between the first series of lacunæ and the Haversian canals. Each lacuna presents eighteen to twenty canaliculi radiating from its borders. The length of the canaliculi is $\frac{1}{800}$ to $\frac{1}{600}$ of an inch (30 to 40 $\mu$), and their diameter is about $\frac{1}{25000}$ of an inch (1 $\mu$). The arrangement and relations of the Haversian canals, lacunæ and canaliculi are shown in Fig. 160.

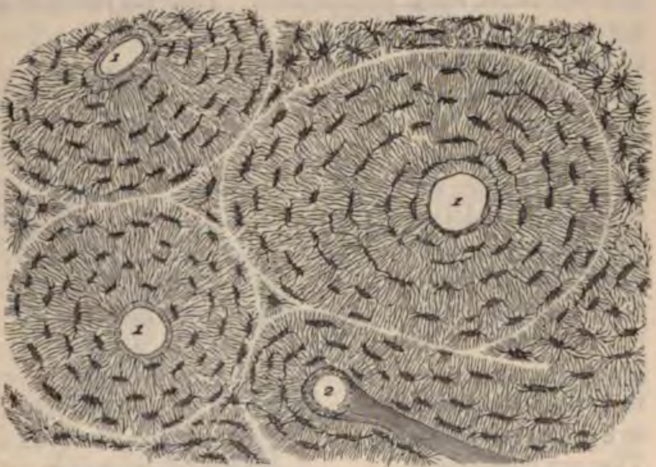


FIG. 160.—*Vascular canals and lacunæ, seen in a transverse section of the humerus; magnified 200 diameters* (Sappey).

1, 1, 1, section of the Haversian canals; 2, section of a longitudinal canal divided at the point of its anastomosis with a transverse canal. Around the canals, cut across perpendicularly, are seen the lacunæ (with their canaliculi), forming concentric rings.

*Bone-cells or Corpuscles.*—These structures are stellate, granular, with a large nucleus and several nucleoli, and are of exactly the size and form of the lacunæ. They send out prolongations into the canaliculi, but it has been impossible to ascertain positively whether or not they form membranes lining the canaliculi throughout their entire length.

*Marrow of the Bones.*—The marrow is found in the medullary cavities of the long bones, filling them completely and moulded to all the irregularities of their walls. It is also found filling the cells of the spongy portion. In other words, with the exception of the vascular canals, lacunæ and canaliculi, the marrow fills all the spaces in the fundamental substance. The cavities of the bones are not lined with a membrane corresponding to the periosteum, and the marrow is applied directly to the bony substance. In the fœtus and in very young children the marrow is red and very vascular. In the adult it is yellow in some bones and gray or gelatiniform in others. It contains certain peculiar cells and nuclei, with amorphous matter, adipose vesicles, connective tissue, blood-vessels and nerves. Robin has described little bodies, existing both in the form of cells and free nuclei, called medullocells. These are found in greater or less number in the bones at all ages, but they are more abundant in proportion as the amorphous matter and fat-cells are deficient. The nuclei are spherical, sometimes with irregular borders, generally without nucleoli, finely granular, and $\frac{1}{5000}$ to $\frac{1}{3000}$ of an inch (5 to 8 $\mu$) in diameter. They are insoluble in acetic acid. The cells, which are less abundant than the free nuclei, are spherical or slightly polyhedric, contain a few pale granulations, are rendered pale but are not dissolved by acetic acid, and they measure about $\frac{1}{1700}$ of an inch (15 $\mu$) in diameter. Irregular, nucleated patches, described by Robin under the name of myeloplaxes, more abundant in the spongy portions than in the medullary canals,

FIG. 161.—*Transverse section of bone, from the shaft of the human humerus; magnified 180 diameters* (from a photograph taken at the United States Army Medical Museum).

FIG. 162.—*Bone-corpuscles, with their prolongations* (Rollett).

are found applied to the internal surfaces of the bones. They are very irregular in size and form (measuring $\frac{1}{1200}$ to $\frac{1}{250}$ of an inch, or 20 to 100 $\mu$ in diameter), are finely granular, and present two to twenty or thirty nuclei. The nuclei are clear and ovoid and are generally provided with a distinct nucleolus. The myeloplaxes are rendered pale by acetic acid, and the nuclei are then brought distinctly into view. They are particularly abundant in the red marrow.

In addition to the anatomical elements just described, the marrow contains a few very delicate bundles of connective tissue, most of which accompany the blood-vessels. In the fœtus the adipose vesicles are few or may be absent; but in the adult they are quite abundant, and in some bones they seem to constitute the whole mass of the marrow. They do not differ materially from the fat-cells in other situations. Holding these different structures together, is a variable quantity of semi-transparent, amorphous or slightly granular matter.

The nutrient artery of the bones sends branches to the marrow, generally two in number for the long bones, which are distributed between the various anatomical elements and finally surround the fatty lobules and the fat-vesicles with a delicate capillary plexus. The veins correspond to the arteries in their distribution. The nerves follow the arteries and are lost when these vessels no longer present a muscular coat. Nothing is known of the presence of lymphatics in any part of the bones or in the periosteum.

The chief physiological interest connected with the marrow of the bones is in its relations to the formation of blood-corpuscles. This question has already been discussed in connection with the development of the corpuscular elements of the blood.

*Periosteum.*—In most of the bones the periosteum presents a single layer of fibrous tissue, but in some of the long bones two or three layers may be demonstrated. This membrane adheres to the bone but can generally be separated without much difficulty. It covers the bones completely, except at the articular surfaces, where its place is supplied by cartilaginous incrustation. It is composed mainly of ordinary fibrous tissue with small elastic fibres, blood-vessels, nerves and a few adipose vesicles.

The arterial branches ramifying in the periosteum are quite abundant, forming a close, anastomosing plexus, which sends small branches into the bony substance. There is nothing peculiar in the arrangement of the veins. The distribution of the veins in the bony substance itself has been very little studied.

The nerves of the periosteum are very abundant and form in its substance quite a close plexus.

The adipose tissue is very variable in quantity. In some parts it forms a continuous sheet, and in others the vesicles are scattered here and there in the substance of the membrane.

The importance of the periosteum to the nutrition and regeneration of the bones is very great. Instances are on record where bones have been removed, leaving the periosteum, and in which the entire bone has been

FIG. 163.—*Section of cartilage from the rib of the ox, showing the homogeneous fundamental substance, cartilage-cavities and cartilage-cells; magnified 370 diameters* (from a photograph taken at the United States Army Medical Museum).

regenerated. The importance of the periosteum has been still farther illustrated by the experiments of Ollier and others, upon transplantation of this membrane in the different tissues of living animals, which has been followed by the formation of bone in these situations.

*Physiological Anatomy of Cartilage.*—In this connection the structure of the articular cartilages presents the chief physiological interest. The articular surfaces of all the bones are encrusted with a layer of cartilage, varying in thickness between $\frac{1}{50}$ and $\frac{1}{25}$ of an inch (0·5 and 1 mm.). The cartilaginous substance is white, opaline, and semi-transparent when examined in thin sections. It is not covered with a membrane, but in the non-articular cartilages it has an investment analogous to the periosteum.


FIG. 164.—*Perpendicular section of a diarthrodial cartilage* (Sappey).

1, 1, osseous tissue; 2, 2, superficial layer of osseous tissue treated with hydrochloric acid; 3, 3, cavities and cells of the deep layer of cartilage; 4, 4, cavities and cells of the middle layer; 5, 5, cavities and cells of the superficial layer.

Examined in thin sections, cartilage is found to consist of a homogeneous fundamental substance, marked with excavations, called cartilage-cavities or chondroplasts. The intervening substance has a peculiar organic constituent, called chondrine. The organic matter is united with a certain proportion of inorganic salts. This fundamental substance is elastic and resisting. The cartilages are closely united to the subjacent bony tissue. The free articular surface has already been described in connection with the synovial membranes.

*Cartilage-Cavities.*—These cavities are rounded or ovoid, measuring $\frac{1}{1250}$ to $\frac{1}{300}$ of an inch (20 to 80 $\mu$) in diameter. They are generally smaller in the articular cartilages than in other situations, as in the costal cartilages. They are simple excavations in the fundamental substance, have no lining membrane, and they contain a small quantity of a viscid liquid with one or more cells. They are analogous to the lacunæ of the bones.

*Cartilage-Cells.*—Near the surface of the articular cartilages the cavities contain each a single cell; but in the deeper portions the cavities are long and contain two to twenty cells arranged longitudinally. The cells are of about the size of the smallest cavities. They are ovoid, with a large, granular nucleus. They often contain a few small globules of oil. In the costal cartilages the cavities are not abundant but are rounded and quite large. The cells contain generally a certain quantity of fatty matter. The appearance of the ordinary articular cartilage is represented in Fig. 164.

The ordinary cartilages have neither blood-vessels, lymphatics nor nerves, and are nourished by imbibition from the surrounding parts. In the development of the body, the anatomy of the cartilaginous tissue possesses peculiar importance, from the fact that the deposition of cartilage, with a few exceptions, precedes the formation of bone.

*Fibro-Cartilage.*—This variety of cartilage presents certain important peculiarities in the structure of its fundamental substance. It exists in the synchondroses, the cartilages of the ear and of the Eustachian tubes, the interarticular disks, the intervertebral cartilages, the cartilages of Santorini and of Wrisberg, and the epiglottis.

Fibro-cartilage is composed of true fibrous tissue with a great predominance of elastic fibres, fusiform, nucleated fibres, a certain number of adipose

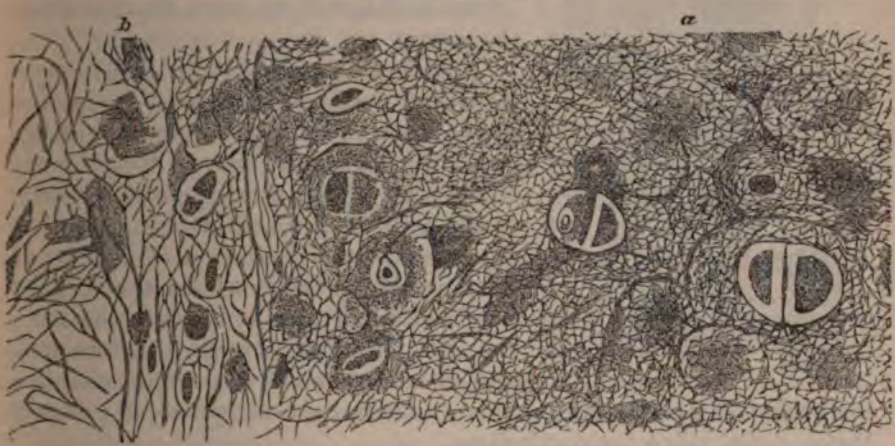



FIG. 165.—*Section of the cartilage of the ear of the human subject* (Rollett).
*a*, fibro-cartilage; *b*, connective tissue. In this preparation, the cartilage had been boiled and dried.

vesicles, cartilage-cells, blood-vessels and nerves (Sappey). The fibrous elements above mentioned take the place of the homogeneous fundamental substance of the true cartilage. The most important peculiarity in the structure of this tissue is that it is abundantly supplied with blood-vessels and nerves.

The reader is referred to works upon anatomy for a history of the action of the muscles. In some works upon physiology, will be found descriptions of the acts of walking, running, leaping, swimming etc.; but it has been thought better to omit these subjects, rather than to enter so minutely as would be necessary into anatomical details and to give elaborate descriptions of movements that are simple and familiar.


Fig. 166.—*Longitudinal section of the human larynx, showing the vocal chords* (Sappey).

1, ventricle of the larynx; 2, superior vocal chord; 3, inferior vocal chord; 4, arytenoid cartilage; 5, section of the arytenoid muscle; 6, 6, inferior portion of the cavity of the larynx; 7, section of the posterior portion of the cricoid cartilage; 8, section of the anterior portion of the cricoid cartilage; 9, superior border of the cricoid cartilage; 10, section of the thyroid cartilage; 11, 11, superior portion of the cavity of the larynx; 12, 13, arytenoid gland; 14, 16, epiglottis; 15, 17, adipose tissue; 18, section of the hyoid bone; 19, 19, 20, trachea.

## Voice and Speech.

The principal organ concerned in the production of the voice is the larynx. The accessory organs are the lungs, trachea, expiratory muscles, the mouth and the resonant cavities about the face. The lungs furnish the air by which the vocal chords are thrown into vibration, and the mechanism of this action is merely a modification of expiration. By the action of the expiratory muscles the intensity of vocal sounds is regulated. The trachea not only conducts the air to the larynx, but it may assist, by resonance, in modifying the quality of the voice. Most of the variations in the tone and quality, however, are effected by the action of the larynx itself and of the parts situated above the larynx.

*Sketch of the Physiological Anatomy of the Vocal Organs.*—The vocal chords are stretched across the superior opening of the larynx from before backward. They consist of two pairs. The superior, called the false vocal chords or the ventricular bands, are not concerned in the production of the voice. They are less prominent than the inferior chords, although they have nearly the same direction. They are covered by a thin mucous membrane, which is closely adherent to the subjacent tissue. The chords themselves are composed of ordinary fibrous tissue, with a few elastic fibres.

The true vocal chords, or vocal bands, are situated just below the superior chords. Their anterior attachments are near together, at the middle of the thyroid cartilage, and are immovable. Posteriorly they are attached to the movable arytenoid cartilages; and by the action of certain muscles, their tension may be modified and the chink of the glottis may be opened or closed. These are much larger than the false vocal chords, and they contain a great number of elastic fibres. Like the superior vocal chords, they are covered with a very thin and closely adherent mucous membrane. The mucous membrane over the borders of the chords is covered with flattened epithelium without cilia. There are no mucous glands in the membrane covering either the superior or the inferior chords. The inferior vocal chords alone are concerned in the production of the voice.

*Muscles of the Larynx.*—The muscles of the larynx are classified as extrinsic and intrinsic. The extrinsic muscles are attached to the outer surface of the larynx and to adjacent organs, such as the hyoid bone and the sternum. They are concerned chiefly in the movements of elevation and depression of the larynx. The intrinsic muscles are attached to the different parts of the larynx itself, and by their action upon the articulating cartilages, are capable of modifying the condition of the vocal chords.

The vocal chords can be rendered tense or loose by muscular action. Their fixed point is in front, where their extremities, attached to the thyroid cartilage, are nearly or quite in contact with each other. The arytenoid cartilages, to which they are attached posteriorly, present a movable articulation with the cricoid cartilage; and the cricoid, which is narrow in front, and is wide behind, where the arytenoid cartilages are attached, presents a movable articulation with the thyroid cartilage. It is evident, therefore, that muscles acting upon the cricoid cartilage can cause it to swing upon its two points of articulation with the inferior cornua of the thyroid, raising the anterior portion and approximating it to the lower edge of the thyroid; and as a consequence, the posterior portion, which carries the arytenoid cartilages and the posterior attachments of the vocal chords, is depressed. This action would, of course, increase the distance between the arytenoid cartilages and the anterior portion of the thyroid, elongate the vocal chords, and subject them to a certain degree of tension. Experiments have shown that such an effect is produced by the contraction of the crico-thyroid muscles.


FIG. 167.—*Posterior view of the muscles of the larynx* (Sappey).
1, posterior crico-arytenoid muscle; 2, 3, 4, different fasciculi of the arytenoid muscle; 5, aryteno-epiglottidean muscle.

The articulations of the different parts of the larynx are such that the arytenoid cartilages may be approximated to each other posteriorly, thus diminishing the interval between the posterior attachments of the vocal chords. This action can be effected by contraction of the single muscle of the larynx (the arytenoid) and also by the lateral crico-arytenoid muscles. The thyro-arytenoid muscles, the most complicated of all the intrinsic muscles in their attachments and the direction of their fibres, are important in regulating the tension and capacity of vibration of the vocal chords.

The posterior crico-arytenoid muscles, arising from each lateral half of the posterior surface of the cricoid cartilage and passing upward and outward to be inserted into the outer angle of the inferior portion of the arytenoid cartilages, rotate these cartilages outward, separate them, and act as dilators of the chink of the glottis. These muscles are chiefly concerned in the respiratory movements during inspiration.

FIG. 168.—*Lateral view of the muscles of the larynx* (Sappey).

1, body of the hyoid bone; 2, vertical section of the thyroid cartilage; 3, horizontal section of the thyroid cartilage, turned downward to show the deep attachment of the crico-thyroid muscle; 4, facet of articulation of the small cornu of the thyroid cartilage with the cricoid cartilage; 5, facet on the cricoid cartilage; 6, superior attachment of the crico-thyroid muscle; 7, posterior crico-arytenoid muscle; 8, lateral crico-arytenoid muscle; 9, thyro-arytenoid muscle; 10, arytenoid muscle; 11, aryteno-epiglottidean muscle; 12, middle thyro-hyoid ligament; 13, lateral thyro-hyoid ligament.

The muscles mainly concerned in the modifications of the voice by their action upon the vocal chords, are the crico-thyroids, the arytenoid, the lateral crico-arytenoids and the thyro-arytenoids. The following is a sketch of their attachments and mode of action:

*Crico-thyroid Muscles.*—These muscles are situated on the outside of the larynx, at the anterior and lateral portions of the cricoid cartilage. Each muscle is of a triangular form, the base of the triangle presenting posteriorly. It arises from the anterior and lateral portions of the cricoid cartilage, and its fibres diverge to be inserted into the inferior border of the thyroid cartilage, extending from the middle of this border posteriorly, as far back as the inferior cornua. Longet, after dividing the nervous filaments distributed to these muscles, noted a certain degree of hoarseness of the voice due to relaxation of the vocal chords; and by imitating their action mechanically, he approximated the cricoid and thyroid cartilages in front, carried back the arytenoid cartilages and rendered the chords tense.

*Arytenoid Muscle.*—This single muscle fills up the space between the two arytenoid cartilages and is attached to their posterior surface and borders. Its action evidently is to approximate the posterior extremities of the chords and to constrict the glottis, as far as the articulations of the arytenoid cartilage with the cricoid will permit. In any event, this muscle is important in phonation, as it serves to fix the posterior attachments of the vocal chords and to increase the efficiency of certain of the other intrinsic muscles.

*Lateral Crico-arytenoid Muscles.*—These muscles are situated in the interior of the larynx. They arise from the sides and superior borders of the cricoid cartilage, pass upward and backward, and are attached to the base of the arytenoid cartilages. By dividing all the filaments of the recurrent laryngeal nerves, except those distributed to these muscles, and then stimulating the nerves, Longet has shown that they act to approximate the vocal chords, and that they constrict the glottis, particularly in its interligamentous portion. These muscles, with the arytenoid, act as constrictors of the larynx.

*Thyro-arytenoid Muscles.*—These muscles are situated within the larynx. They are broad and flat, and they arise in front from the upper part of the crico-thyroid membrane and the lower half of the thyroid cartilage. From this line of origin, each muscle passes backward in two fasciculi, both of which are attached to the anterior surface and the outer borders of the arytenoid cartilages. Stimulation of the nervous filaments distributed to these muscles renders the vocal chords tense. The great variations that may be produced in the pitch and quality of the voice by the action of muscles operating directly or indirectly upon the vocal chords render the problem of determining the precise mode of action of the intrinsic muscles of the larynx complicated and difficult. It is certain, however, that in these muscular acts, the thyro-arytenoids play an important part. Their contraction regulates the thickness of the vocal chords, while at the same time it modifies their tension. The swelling of the chords, which may be rendered regular and progressive under the influence of the will, is one of the most important elements in the formation of the timbre of the voice.

*Mechanism of the Production of the Voice.*—If the glottis be examined with the laryngoscope during ordinary respiration, the wide opening of the chink during forced inspiration, due to the action of the posterior crico-arytenoid muscles, can be observed without difficulty. This action is effected by a separation of the posterior points of attachment of the vocal chords to the arytenoid cartilages. During ordinary expiration, none of the intrinsic muscles seem to act and the larynx is entirely passive, while the air is gently forced out by the elasticity of the lungs and of the thoracic walls; but so soon as an effort is made to produce a vocal sound, the appearance of the glottis undergoes a change, and it becomes modified in the most varied manner with the different changes in pitch and intensity that the voice can be made to assume. Although sounds may be produced, and even words may be articulated, with the act of inspiration, true and normal phonation takes place during expiration only. It is evident, also, that the inferior vocal chords alone are concerned in this act.

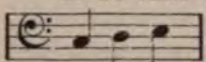
*Movements of the Glottis during Phonation.*—It is somewhat difficult to observe with the laryngoscope all of the vocal phenomena, on account of the epiglottis, which hides a considerable portion of the vocal chords anteriorly, especially during the production of certain notes; but the patience and skill of Manuel Garcia, a celebrated teacher of singing, enabled him to overcome most of these difficulties, and to settle, by autolaryngoscopy, certain important questions with regard to the action of the larynx in singing. It is fortunate that these observations were made by one versed theoretically and practically in music and possessed of great control over the vocal organs.

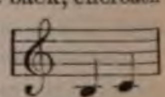
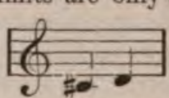
Garcia, after having observed the respiratory movements of the larynx, as they have just been briefly described, noted that as soon as any vocal effort was made, the arytenoid cartilages were approximated, so that the glottis appeared as a narrow slit formed by two chords of equal length, firmly attached posteriorly as well as anteriorly. The glottis thus undergoes a marked change. A nearly passive organ, opening for the passage of air into the lungs but entirely inactive in expiration, has now become a musical instrument, presenting a slit with borders capable of accurate vibrations.

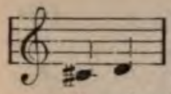
The approximation of the posterior extremities of the vocal chords and their tension by the action of certain of the intrinsic muscles are accomplished just before the vocal effort is actually made. The glottis being thus prepared for the emission of a particular sound, the expiratory muscles force air through the larynx with the required power. The power of the voice is due simply to the force of the expiratory act, which is regulated chiefly by the antagonistic relations of the diaphragm and the abdominal muscles. From the fact that the diaphragm, as an inspiratory muscle, is exactly opposed to the muscles which have a tendency to push the abdominal organs, with the diaphragm over them, into the thoracic cavity and thus to diminish the pulmonary capacity, the expiratory and inspiratory acts may be balanced so nicely that the most delicate vocal vibrations can be produced. The glottis, thus closed as a preparation to a vocal act, presents a certain resistance to the egress of air. This is overcome by the action of the expiratory muscles, and with the passage of air through the chink, the edges of the opening, which are formed by the true vocal chords, are thrown into vibration. Many of the different qualities that are recognized in the human voice are due to differences in the length, breadth and thickness of the vibrating bands; but aside from what is technically known as quality, the pitch is dependent upon the length of the opening through which the air is made to pass and the degree of tension of the chords. The mechanism of these changes in the pitch of vocal sounds is illustrated by Garcia in the following, which relates to what is known as the chest-voice:

FIG. 169. — *Glottis seen with the laryngoscope during the emission of high-pitched sounds* (Le Bon).

1, 2, base of the tongue; 3, 4, epiglottis; 5, 6, pharynx; 7, arytenoid cartilages; 8, opening between the true vocal chords; 9, aryteno-epiglottidean folds; 10, cartilage of Santorini; 11, cuneiform cartilage; 12, superior vocal chords; 13, inferior vocal chords.

"If we emit veiled and feeble sounds, the larynx opens at the notes  and we see the glottis agitated by large and loose vibrations throughout its entire extent. Its lips comprehended in their length the anterior apophyses of the arytenoid cartilages and the vocal chords; but, I repeat it, there remains no triangular space.

"As the sounds ascend, the apophyses, which are slightly rounded on their internal side, by a gradual apposition commencing at the back, encroach on the length of the glottis; and as soon as we reach the sounds  they finish by touching each other throughout their whole extent; but their summits are only solidly fixed one against the other at the notes  In some organs these summits are a little vacillating when they form the posterior end of the glottis, and two or three half-tones which are formed show a certain want of purity and strength, which is very well known to singers. From


the vibrations, having become rounder and purer, are accomplished by the vocal ligaments alone, up to the end of the register.

"The glottis at this moment presents the aspect of a line swelled toward its middle, the length of which diminishes still more as the voice ascends. We shall also see that the cavity of the larynx has become very small, and that the superior ligaments have contracted the extent of the ellipse to less than one-half."

These observations have been in the main confirmed by Battaille, Emma Seiler and others who have applied the laryngoscope to the study of the voice in singing.

In childhood the general characters of the voice are essentially the same in both sexes. The larynx is smaller than in the adult, and the vocal muscles are more feeble; but the quality of the vocal sounds at this period of life is peculiarly penetrating. While there are certain characters that distinguish the voices of boys before the age of puberty, they present, as in the female, the different qualities of the soprano and contralto. After the age of puberty, the female voice does not commonly undergo any very marked change, except in the development of additional strength and increased compass, the quality remaining the same; but in the male there is a rapid change at this time in the development of the larynx, and the voice assumes an entirely different quality. This change does not usually take place if castration be performed in early life; and this operation was frequently resorted to in the seventeenth century, for the purpose of preserving the qualities of the male soprano and contralto, particularly for church-music. It is only of late years, indeed, that this practice has fallen into disuse in Italy.

The ordinary range of all varieties of the human voice is equal to nearly four octaves; but it is rare that any single voice has a compass of more than two and a half octaves. There are examples, however, in which singers have acquired a compass of three octaves. In music the notes are written the same for the male as for the female voice, but the actual value of the female notes, as reckoned by the number of vibrations in a second, is always an octave higher than the male.

In both sexes there are differences, both in the range and the quality of the voice, which it is impossible for a cultivated musical ear to mistake. The different voices in the male are the bass, the tenor, and an intermediate voice called the barytone. The female voices are the contralto, the soprano, and the intermediate, or mezzo-soprano. In the bass and barytone, the lower and middle notes are the most natural and perfect; and while the higher notes may be acquired by cultivation, they do not possess the same quality as the corresponding notes of the tenor. The same remarks apply to the contralto and soprano.

The following scale (Landois) gives the ordinary ranges of the different kinds of voice; but it must be remembered that there are individual instances in which these limits are exceeded:


The accompanying figures indicate the number of vibrations per second in the corresponding tone. It is evident that from *c′* to *f″* is common to all voices; nevertheless, they have a different timbre. The lowest note or tone, which, however, is only occasionally sung by bass singers, is the contra-F, with 42 vibrations; the highest note of the soprano voice is *a‴*, with 1,708 vibrations (Landois and Stirling).

There is really no great difference in the mechanism of the different kinds of voice, and the differences in pitch are due chiefly to the greater length of the vocal chords in the low-pitched voices and to their shortness in the higher voices. The differences in quality are due to peculiarities in the conformation of the larynx, to differences in its size and to variations in the size and form of the auxiliary resonant cavities. Great changes in the quality of the voice may be effected by practice. A cultivated note, for example, has an entirely different sound from a harsh, irregular vibration; and by practice, a tenor may imitate the quality of the bass, and *vice versâ*, although the effort is unnatural. It is not at all unusual to hear male singers imitate very closely the notes of the female, and the contralto will sometimes imitate the voice of the tenor in a surprisingly natural manner.

*Action of the Intrinsic Muscles of the Larynx in Phonation.*—In the production of low chest-notes, in which the vocal chords are elongated and are at the minimum of tension that will allow of regular vibrations, the crico-thyroid muscles are undoubtedly brought into action, and these are assisted by the arytenoid and the lateral crico-arytenoids, which combine to fix the posterior attachments of the vibrating ligaments. It will be remembered that the crico-thyroids, by approximating the cricoid and thyroid cartilages in front, increase the distance between the arytenoid cartilages and the anterior attachment of the vocal chords.

As the notes produced by the larynx become higher in pitch, the posterior attachments of the chords are approximated, and at this time the lateral crico-arytenoids are probably brought into vigorous action.

The uses of the thyro-arytenoids are more complex; and it is probably in great part by the action of these muscles that the varied and delicate modifications in the rigidity of the vocal chords are produced.

The differences in singers as regards the purity of their notes are due in part to the accuracy with which some put the vocal chords upon the stretch; while in those in whom the voice is of inferior quality, the action of the muscles is more or less vacillating and the tension is frequently incorrect.

The fact that some singers can make the voice heard above the combined sounds from a large chorus and orchestra is not due entirely to the intensity of the sound, but in a great measure to the mathematical equality of the sonorous vibrations and the comparative absence of discordant waves.

*Action of Accessory Vocal Organs.*—A correct use of the accessory organs of the voice is of great importance in singing; but the action of these parts is simple and does not require a very extended description. The human vocal organs, indeed, consist of a vibrating instrument, the larynx, and of certain tubes and cavities by which the sound is re-enforced and modified.

The trachea serves, not only to conduct air to the larynx, but to re-enforce the sound to a certain extent by the vibrations of the column of air in its interior. When a powerful vocal effort is made, it is easy to feel, with the finger upon the trachea, that the contained air is thrown into vibration.

The capacity of the cavity of the larynx is capable of certain variations. In fact, both the vertical and the bilateral diameters are diminished in high notes and are increased in low notes. The vertical diameter may be modified slightly by ascent and descent of the true vocal chords, and the lateral diameter may be reduced by the action of the inferior constrictors of the pharynx upon the sides of the thyroid cartilage.

The epiglottis, the superior vocal chords and the ventricles are by no means indispensable to the production of vocal sounds. In the emission of high notes the epiglottis is somewhat depressed, and the superior chords are brought nearer together; but this affects the form of the resonant cavity only above the glottis. In low notes the superior chords are separated. It was before the use of the laryngoscope in the study of vocal phenomena that the epiglottis and the ventricles were thought to be so important in phonation. Undoubtedly, the epiglottis has something to do with the character of the voice; but its action is not absolutely necessary or even very important, as has been shown in experiments of excising the part in living animals.

The most important modifications of the laryngeal sounds are produced by the resonance of air in the pharynx, mouth and nasal fossæ. This resonance is indispensable to the production of the natural, human voice. Under ordinary conditions, in the production of low notes the velum palati is fixed by the action of its muscular fibres, so that there is a reverberation of the bucco-pharyngeal and naso-pharyngeal cavities; that is, the velum is in such a position that neither the opening into the nose nor the opening into the mouth is closed, and all of the cavities resound. As the notes are raised in pitch, the isthmus contracts, the part immediately above the glottis is also constricted, the resonant cavity of the pharynx and mouth is reduced in size, until finally, in the highest notes of the chest-register, the communication between the pharynx and the nasal fossæ is closed, and the sound is re-enforced entirely by the pharynx and mouth. At the same time the tongue—a very important organ to singers, particularly in the production of high notes—is drawn backward. The point being curved downward, its base projects upward posteriorly and assists in diminishing the capacity of the bucco-pharyngeal cavity. In the changes which the pharynx thus undergoes in the production of different notes, the uvula acts with the velum and assists in the closure of the different openings. In singing up the scale, this is the mechanism, as far as the chest-notes extend. When, however, a singer changes into what is sometimes called the head-voice (falsetto), the velum palati is drawn forward instead of backward, and the resonance takes place chiefly in the naso-pharyngeal cavity.

*Laryngeal Mechanism of the Vocal Registers.*—One difficulty at the very beginning of a discussion of this subject is in fixing upon clear definitions of what are to be recognized as different vocal registers. In the first place it must be understood that the singing voice is very different from the speaking voice. Without being actually so far discordant as to offend a musical ear, the ordinary voice in speaking never has what may strictly be called a musical quality, while the perfect singing voice produces true musical notes. This is probably due to the fact that the inflections of the voice in speaking are not in the form of distinct musical intervals, that the vibrations follow each other and are superimposed in an irregular manner, and that no special effort is made to put the vocal chords upon any definite tension, unless to meet a more powerful expiratory effort when the voice is increased in force. A shout or a scream is entirely different from a powerful, singing note. This difference is at once apparent in contrasting recitative with ordinary dialogue in operatic performances.

The divisions of the voice into registers, made by physiologists, are sometimes based upon theories with regard to the manner of their production; and if these theories be not correct, the division into registers must be equally faulty. Again, there are such marked differences between male and female voices, that it does not seem possible to apply the same divisions to both sexes. There is no difficulty, however, in recognizing the qualities of voice, called bass, barytone and tenor, in the male, or contralto, mezzo and soprano, in the female. A division of the voice into registers should be one easily recognizable by singers and singing teachers; and this must be different for male and female voices. If a division were made such as would be universally recognized by the ear, irrespective of theories, it would remain only to ascertain as nearly as possible the exact vocal mechanism of each register. It must be remembered that the voice of a perfect singer shows no recognizable break, or line of division between the vocal registers, except when a difference is made apparent in order to produce certain legitimate musical effects. One great end sought to be attained in training the voice in singing is to make the voice as nearly as possible uniform throughout the extent of its range; and this has been measurably accomplished in certain singers.

Judging of different registers entirely by the effect produced upon the ear, both by cultivated and uncultivated singers, the following seem to be the natural divisions of the male voice:

1. The chest-register. This is the register commonly used in speaking. Though usually called the chest-voice, it has, of course, no connection with any special action of the chest, except, perhaps, with reverberation of air in

the trachea and the larger bronchial tubes. This register is sensibly the same in the male and in the female.

2. The head-register. In cultivated male voices, a quality is often produced, probably by diminished power of the voice, with some modification in the form and capacity of the resonant cavities, which is recognized as a "head-voice," by those who do not regard the head-register as equivalent to the falsetto.

3. The falsetto-register. By the use of this register, the male may imitate the voice of the female. Its quality is different from that of the chest-voice, and the transition from the chest to falsetto usually is abrupt and quite marked. It may be called an unnatural voice in the male; still, by very careful cultivation, the transition may be made almost imperceptibly. The falsetto never has the power and resonance of the full chest-voice. It resembles the head-voice, but every good singer can recognize the fact that he employs a different mechanism in its production.

Applying an analogous method of analysis to the female voice, the natural registers seems to be the following:

1. The chest-register. This register is the same in the female as in the male.

2. The lower medium register, generally called the medium. This is the register commonly used by the female in speaking.

3. The upper medium register. This is sometimes called the head-register and is thought by some to be produced by precisely the same mechanism as the falsetto-register in the male. It has, however, a vibrant quality, is full and powerful, and is not an unnatural voice like the male falsetto.

4. The true head-register. This is the pure tone, without vibrant quality, which seems analogous to the male falsetto.

*Vocal Registers in the Male.*—According to the division and definitions just given of the vocal registers, in the male voice there is but one register, extending from the lowest note of the bass to the falsetto, and this is the chest-register. In the low notes, the vocal chords vibrate, and the arytenoid cartilages participate in this vibration to a greater or less extent. In the low notes, also, the larynx is open; that is, the arytenoid cartilages do not touch each other. As the notes are raised in pitch, the arytenoid cartilages are approximated more and more closely, and they touch each other in the highest notes, the vocal chords vibrating alone. It is probable that the degree of approximation of the arytenoid cartilages is different in different singers, and that the part of the musical scale at which they actually touch is not invariable. This appears to be the case in the observations made by Mills.

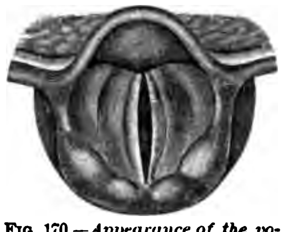


FIG. 170.—*Appearance of the vocal chords in the production of the chest-voice, after Mandl* (Grützner.)

What has been called, in this classification, the head-register of the male, is not a full, round voice, but the notes are more or less *sotto voce*. This peculiar quality of voice does not seem to have been made the subject of laryngoscopic investigation. It has a vibrant character, which is undoubtedly modified by peculiar action of the resonant cavities, which latter has not been described. It is not probable that its mechanism differs essentially, as regards the action of the glottis, from that of the full chest-register, shown in Fig. 170.

The falsetto-register in the male undoubtedly involves such a division of the length of the vocal chords that only a portion is thrown into vibration. There is always an approximation of the chords in their posterior portion, and sometimes also in their anterior portion. This is illustrated in Fig. 171.


FIG. 171.—*Appearances of the vocal chords in the production of the falsetto-voice* (Mills).
I. The larynx during falsetto production; after Mandl.
II. The larynx during the emission of falsetto tones; middle range; after Holmes.
III. The larynx of the female during the production of head-tones, as seen by the author (Mills).

The mechanism by which the vocal chords are approximated in portions of their length has not been satisfactorily explained; but laryngoscopic examinations leave no doubt of the fact of such action. The extent of this shortening of the chords must vary in different persons and in the same person, probably, in the production of falsetto-notes of different pitch. According to Mrs. Seiler, the shortening is due to the action of a muscular bundle, called the internal thyro-arytenoid, upon little cartilages extending forward from the arytenoid cartilage, in the substance of the vocal chords, as far as the middle of the glottis; but dissections made by Mills failed to confirm this view.

Some singers, especially tenors, have been able by long practice to pass from the chest to the falsetto so skillfully that the transition is scarcely apparent, but the falsetto is devoid of what is called vibrant quality.

*Vocal Registers in the Female.*—There is absolutely no difference between the vocal mechanism of the chest-voice in the sexes. In the best methods of teaching singing, one important object is to smooth the transition from the chest-voice to the lower medium. The full chest-notes, especially in contraltos, closely resemble the corresponding notes of the tenor.

According to the laryngoscopic observations of Mills, the mechanism of the lower medium and upper medium in females does not radically differ from the mechanism of the chest-voice. In these registers, the arytenoid cartilages become more and more closely approximated to each other as the voice ascends in the scale until, in the higher notes, they probably are firmly in apposition. It is probable that the vocal chords alone vibrate in the lower and upper medium, while the apophyses of the arytenoid cartilages participate in the vibrations in the female chest-voice.

The vocal chords are much shorter in the female than in the male. According to Sappey, the average length in the male is about $\frac{7}{8}$ of an inch (22 mm.) and in the female, about $\frac{5}{8}$ of an inch (17 mm.). If the chords alone vibrate, without the apophyses of the arytenoid cartilages, the difference in length would account for the differences in pitch of the voice in the sexes. The tenor can not sing above the chest-range of the female voice without passing into the falsetto, to produce which he must actually shorten his vocal chords so that they are as short or shorter than the vocal chords of the female. This is shown by the scale of range of the different voices compared with the length of the vocal chords; and this idea is sustained still farther by a comparison of "the larynx during falsetto production" (Fig. 171, I). In the male falsetto, produced by this shortening of the vocal chords, the more nearly the resonant cavities are made to resemble, in form and capacity, the corresponding cavities in the female, the more closely will the quality of the female voice be imitated. It is probable that the vocal bands in the female present a thinner and narrower vibrating edge than the chords in the male, although there are no exact anatomical observations on this point. This would account for the clear quality of the upper registers of the female voice as compared with the male voice or with the female chest-register. Analogous differences exist in reed-instruments, such as the clarinet and the bassoon. This comparison of the female upper registers with the male falsetto does not necessarily imply a similarity in the mechanism of their production, as is assumed by some writers. The vocal chords, in the female lower and upper medium, vibrate in their entire length; in the male falsetto, the chords are artificially shortened so that they are approximated in length to the length of the chords in the female.

To reduce to brief statements the views just expressed, based partly upon laryngoscopic examinations—that are far from complete—by a number of competent observers, the following may be given as the mechanism of the vocal registers in the female, taking no account of the changes in form and capacity of the resonant cavities:

1. The chest-voice is produced by "large and loose vibrations" (Garcia) of the entire length of the vocal chords, in which the apophyses of the arytenoid cartilages participate to a greater or less extent, these cartilages not being in close apposition.

2. In passing to the lower medium, the arytenoid cartilages probably are not closely approximated, but they do not vibrate, the vocal chords alone acting.

3. In passing to the upper medium, the arytenoid cartilages probably are closely approximated, and the vocal chords alone vibrate, but they vibrate in their entire length.

4. The head-register, which may be called the female falsetto, bears the same relation to the lower registers in both sexes. The notes are clear but

deficient in vibrant quality. They are higher in the female than in the male because the vocal chords are shorter. Laryngoscopic observations demonstrating this fact in the female are as accurate and definite as in the male. (See Fig. 171.)

The reasons why the range of the different vocal registers is limited are the following: Within the limits of each register, the tension of the vocal chords has an exact relation to the pitch of the sound produced. This tension is of course restricted by the limits of power of the muscles acting upon the vocal chords, for high notes, and by the limit of possible regular vibration of chords of a certain length, for low notes. The higher the tension and the greater the rigidity of the chords, the greater is the force of air required to throw them into vibration; and this, also, has, of course, certain limits. It is never desirable to push any of the lower registers in female voices to their highest limits. All competent singing teachers recognize this fact. The female chest-register may be made to meet the upper medium, particularly in contraltos; but the singer then has practically two voices, a condition which is musically intolerable. In blending the different registers so as to make a perfectly uniform, single voice, the arytenoid vibrations should be rendered progressively and evenly less and less prominent, until they imperceptibly cease when the lower medium is fully reached; the arytenoid cartilages should then be progressively and evenly approximated to each other, until they are firmly in contact and the upper medium is fully reached. The female vocal apparatus is then perfect. While single notes of the chest, lower medium and upper medium, contrasted with each other, have different qualities, the voice is even throughout its entire range, and the proper shading called for in musical compositions can be made in any part of the scale. The blending of the male chest-register into the falsetto and of the upper medium into the female falsetto, or true head-voice, is more difficult, but it is not impossible. Theoretically, this must be done by shortening the vocal chords gradually and progressively and not abruptly, unless the latter be required to produce a legitimate effect of contrast.

Even in singing identical notes, there are distinctly recognizable differences in quality between the bass, barytone and tenor, and between the contralto, mezzo and soprano. For the female, these may be compared to the differences in identical notes played on different strings of the violin. For the male, they may be compared to the qualities of the different strings of the violoncello. Falsetto-notes may be compared to harmonics produced on these instruments.

These ideas with regard to the mechanism of the different vocal registers have resulted from a study of these registers, first from an æsthetic point of view; endeavoring then to find explanations of different qualities of sound appreciated by the ear, in laryngoscopic and other scientific observations, and not by reasoning from scientific observations, as to what effects upon the ear should be produced by certain acts performed by the vocal organs. It may be stated, in this connection, that the works of Bach, Beethoven and other old masters were composed, exactly in accordance with purely physical laws, long before these laws were ascertained and defined, as has lately been done, particularly by Helmholtz.

MECHANISM OF SPEECH.

Articulate language consists in a conventional series of sounds made for the purpose of conveying certain ideas. There being no universal language, it will be necessary to confine the description of speech to the language in which this work is written. Language, as it is naturally acquired, is purely imitative and does not involve of necessity the construction of an alphabet, with its combinations into syllables, words and sentences; but as civilization has advanced, certain differences in the accuracy and elegance with which ideas are expressed have become associated with the degree of development and cultivation of the intellectual faculties. Philologists have long since established a certain standard—varying, to some extent, it is true, with usage and the advance of knowledge, but still sufficiently definite—by which the correctness of modes of expression is measured. It is not proposed to discuss the science of language, or to consider, in this connection at least, the peculiar mental operations concerned in the expression of ideas, but to take the language as it exists, and to describe briefly the mechanism of the production of the most important articulate sounds.

Almost every language is imperfect, as far as an exact correspondence between its sounds and written characters is concerned. The English language is full of incongruities in spelling, such as silent letters and arbitrary and unmeaning variations in pronunciation; but these do not belong to the subject of physiology. There are, however, certain natural divisions of the sounds as expressed by the letters of the alphabet.

*Vowels.*—Certain articulate sounds are called vowel, or vocal, from the fact that they are produced by the vocal chords and are but slightly modified as they pass out of the mouth. The true vowels, *a*, *e*, *i*, *o*, *u*, can all be sounded alone and may be prolonged in expiration. These are the sounds chiefly employed in singing. The differences in their characters are produced by changes in the position of the tongue, mouth and lips. The vowel-sounds are necessary to the formation of a syllable, and although they generally are modified in speech by consonants, each one may of itself form a syllable or a word. In the construction of syllables and words, the vowels have many different qualities, the chief differences being as they are made long or short. In addition to the modifications in the vowel-sounds by consonants, two or three may be combined so as to be pronounced by a single vocal effort, when they are called respectively, diphthongs and triphthongs. In the proper diphthongs, as *oi*, in voice, the two vowels are sounded. In the improper diphthongs, as *ea*, in heat, and in the Latin diphthongs, as *æ*, in Cæsar, one of the vowels is silent. In triphthongs, as *eau*, in beauty, only one vowel is sounded. *Y*, at the beginning of words, is usually pronounced as a consonant; but in other positions it is pronounced as *e* or *i*.

An important question relates to the differences in the quality of the different vowel-sounds when pronounced with equal pitch and intensity. The cause of these differences was studied very closely in the latter part of the last century, but it has lately been rendered clear by the researches of Helmholtz and of Koenig. In this connection it will be sufficient to indicate the results of the modern investigations very briefly. It will be seen in studying the physics of sound in connection with the sense of hearing, that nearly all sounds, even when produced by a single, vibrating body, are compound. Helmholtz, by means of his resonators, has succeeded in analyzing the apparently simple sounds into different component parts, and he has shown that the quality of such sounds may be modified by re-enforcing certain of the overtones, as they are called, such as the third, fifth or octave. For those who are familiar with the physics of sound, the explanation of the mechanism of the production of vowel-sounds will be readily comprehensible. The reader is referred, however, to the remarks upon overtones in another part of this work, under the head of audition, for a more thorough exposition of this subject. The different vowel-sounds may be emitted with the same pitch and intensity, but the sound in each is different on account of variations in the resonant cavities of the accessory vocal organs, especially the mouth. It has been ascertained experimentally that the overtones in each instance are different, as they are re-enforced by the vibrations of air in the accessory vocal organs, in some instances the third, in others, the fifth etc., being increased in intensity. This can hardly be better illustrated than by the following quotation from Tyndall, in which modern researches have been applied to the vowel-sounds of the English language:

"For the production of the sound *U* (*oo* in hoop), I must push my lips forward so as to make the cavity of the mouth as deep as possible, at the same time making the orifice of the mouth small. This arrangement corresponds to the deepest resonance of which the mouth is capable. The fundamental tone of the vocal chords is here re-enforced, while the higher tones are thrown into the shade. The *U* is rendered a little more perfect when a feeble third tone is added to the fundamental.

"The vowel *O* is pronounced when the mouth is so far opened that the fundamental tone is accompanied by its strong higher octave. A very feeble accompaniment of the third and fourth is advantageous, but not necessary.

"The vowel *A* derives its character from the third tone, to strengthen which by resonance the orifice of the mouth must be wider, and the volume of air within it smaller than in the last instance. The second tone ought to be added in moderate strength, whilst weak fourth and fifth tones may also be included with advantage.

"To produce *E* the fundamental tone must be weak, the second tone comparatively strong, the third very feeble, but the fourth, which is characteristic of this vowel, must be intense. A moderate fifth tone may be added. No essential change, however, occurs in the character of the sound when the third and fifth tones are omitted. In order to exalt the higher tones which characterize the vowel-sound *E*, the resonant cavity of the mouth must be small.

"In the production of the sound *ah!* the higher overtones come principally into play; the second tone may be entirely neglected; the third rendered very feebly; the higher tones, particularly the fifth and seventh, being added strongly.

"These examples sufficiently illustrate the subject of vowel-sounds. We may blend in various ways the elementary tints of the solar spectrum, producing innumerable composite colors by their admixture. Out of violet and red we produce purple, and out of yellow and blue we produce white. Thus also may elementary sounds be blended so as to produce all possible varieties of clang-tint. After having resolved the human voice into its constituent tones, Helmholtz was able to imitate these tones by tuning-forks, and, by combining them appropriately together, to produce the clang-tints of all the vowels."

*Consonants.*—Some of the consonants have no sound in themselves and serve merely to modify vowel-sounds. These are called mutes. They are *b*, *d*, *k*, *p*, *t*, and *c* and *g* hard. Their office in the formation of syllables is sufficiently apparent.

The consonants known as semivowels are *f*, *l*, *m*, *n*, *r*, *s*, and *c* and *g* soft. These have an imperfect sound of themselves, approaching in character the true vowel-sounds. Some of these, *l*, *m*, *n* and *r*, from the facility with which they flow into other sounds, are called liquids. Orthoepists have farther divided the consonants with reference to the mechanism of their pronunciation: *d*, *j*, *s*, *t*, *z*, and *g* soft, being pronounced with the tongue against the teeth, are called dentals; *d*, *g*, *j*, *k*, *l*, *n*, and *q* are called palatals; *b*, *p*, *f*, *v* and *m* are called labials; *m*, *n* and *ng* are called nasals; and *k*, *q*, and *c* and *g* hard are called gutturals. After the description already given of the voice, it is not necessary to discuss farther the mechanism of these simple acts of articulation.

For the easy and proper production of articulate sounds, absolute integrity of the mouth, teeth, lips, tongue and palate is required. All are acquainted with the modifications in articulation in persons in whom the nasal cavities resound unnaturally from imperfection of the palate; and the slight peculiarities observed after loss of the teeth and in harelip are sufficiently familiar. The tongue is generally regarded, also, as an important organ of speech, and this is the fact in the great majority of cases; but instances are on record in which distinct articulation has been preserved after complete destruction of this organ. These cases, however, are unusual, and they do not invalidate the great importance of the tongue in ordinary speech.

It is thus seen that speech consists essentially in a modification of the vocal sounds by the accessory organs, or by parts situated above the larynx; the latter being the true vocal instrument. While the peculiarities of pronunciation in different persons and the difficulty of acquiring foreign languages after the habits of speech have been formed show that the organs of articulation must perform their office with great accuracy, their movements are simple, and they vary with the peculiarities of different languages.

*Whispering.*—Articulate sounds may be produced by the action of the resonant cavities, the lips, teeth and tongue, in which the larynx takes no part.

This action occurs in whispering and it can not properly be called vocal. It is difficult to make any considerable variations in the pitch of a whisper, and articulation in this way may be produced in inspiration as well as in expiration, although the act in expiration is more natural and easy. The character of a whisper may be readily distinguished from that of the faintest audible sound involving vibration of the vocal chords. In aphonia from simple paralysis of the vocal muscles of the larynx, patients can articulate distinctly in whispering; but in cases of chronic bulbar paralysis (glosso-labio-laryngeal paralysis), speech is entirely lost.

*The Phonograph.*—In 1877, a remarkable invention was made in this country, by Mr. Thomas A. Edison, which possesses considerable physiological importance. Mr. Edison constructed a very simple instrument, called the phonograph, which will repeat, with a certain degree of accuracy, the peculiar characters of the human voice both in speaking and singing, as well as the pitch and quality of musical instruments. This demonstrates conclusively the fact that the qualities of vocal sounds depend upon the form of the sonorous vibrations. The following are the main features in the construction of this instrument: It consists of a cylinder of iron provided with very fine, shallow grooves in the form of an exceedingly close spiral. Upon the cylinder, a sheet of tin-foil is accurately fitted. Bearing upon the tin-foil, is a steel-point connected with a vibrating plate of mica or of thin iron. The vibrating plate is connected with a mouth-piece which receives the vibrations of the voice or of a musical instrument. The cylinder is turned with a crank, and at the same time, the plate is thrown into vibration by speaking into the mouth-piece. As the disk vibrates in consonance with the voice, the vibrations are marked by little indentations upon the tin-foil. When this has been done, the cylinder is moved back to the starting point and is turned again at the same rate as before. As the steel-point passes over the indentations in the tin-foil, the plate is thrown into vibration, and the sound of the voice is actually repeated, although much diminished in intensity and distinctness. The improvements that have lately been made in the phonograph do not involve any modifications in the principles of its construction.

# CHAPTER XVI.

## *PHYSIOLOGICAL DIVISIONS, STRUCTURE AND GENERAL PROPERTIES OF THE NERVOUS SYSTEM.*

**Divisions and structure of the nervous tissue—Medullated nerve-fibres—Simple, or non-medullated nerve-fibres—Gelatinous nerve-fibres (fibres of Remak)—Accessory anatomical elements of the nerves—Termination of the nerves in the muscular tissue—Termination of the nerves in glands—Modes of termination of the sensory nerves—Corpuscles of Vater, or of Pacini—Tactile corpuscles—End-bulbs—Structure of the nerve-centres—Nerve-cells—Connection of the cells with the fibres and with each other—Accessory anatomical elements of the nerve-centres—Composition of the nervous substance—Degeneration and regeneration of the nerves—Motor and sensory nerves—Mode of action of the motor nerves—Associated movements—Mode of action of the sensory nerves—Physiological differences between motor and sensory nerve-fibres—Nervous excitability—Different means employed for exciting the nerves—Rapidity of nervous conduction—Personal equation—Action of electricity upon the nerves—Law of contraction—Induced muscular contraction—Electrotonus, anelectrotonus and catelectrotonus—Negative variation.**

THE nervous system is anatomically and physiologically distinct from all other systems and organs in the body. It receives impressions made upon the terminal branches of its sensory portion and it conveys stimulus to parts, determining and regulating their actions; but its physiological properties are inherent, and it gives to no tissue or organ its special excitability or the power of performing its particular office in the economy. The nervous system connects into a co-ordinated organism all parts of the body. It is the medium through which all impressions are received. It animates or regulates all movements, voluntary and involuntary. It regulates secretion, nutrition, calorification and all the processes of organic life.

In addition to its action as a medium of conduction and communication, the nervous system, in certain of its parts, is capable of receiving impressions and of generating a stimulating influence, or force, peculiar to itself. As there can be no physiological connection or co-ordination of different parts of the organism without nerves, there can be no unconscious reception of impressions giving rise to involuntary movements, no appreciation of impressions, general, as in ordinary sensation, or special, as in sight, smell, taste or hearing, no instinct, volition, thought or even knowledge of existence, without nerve-centres.

### DIVISIONS AND STRUCTURE OF THE NERVOUS TISSUE.

The nervous tissue presents two great divisions, each with distinct anatomical as well as physiological differences. One of these divisions is composed of fibres or tubes. This kind of nervous matter is incapable of generating a force or stimulus, and it serves only as a conductor. The other division is composed of cells, and this kind of nervous matter, while it may act as a conductor, is capable of generating the so-called nerve-force.

The nerve-fibres and cells are also divided into two great systems, as follows:

1. The cerebro-spinal system, composed of the brain and spinal cord with the nerves directly connected with these centres. This system is specially connected with the functions of relation, or of animal life. The centres pre-

side over general sensation, the special senses, voluntary and some involuntary movements, intellection, and, in short, all of the functions that characterize the animal. The nerves serve as the conductors of impressions known as general or special sensations and of the stimulus that gives rise to voluntary and certain involuntary movements, the latter being the automatic movements connected with animal life.

2. The sympathetic, or organic system. This system is specially connected with the functions relating to nutrition, operations which have their analogue in the vegetable kingdom and are sometimes called the functions of vegetative life. Although this system presides over functions entirely distinct from those characteristic of and peculiar to animals, the centres of this system all have an anatomical and physiological connection with the cerebro-spinal nerves.

The cerebro-spinal system is subdivided into centres presiding over movements and ordinary sensation, and centres capable of receiving impressions connected with the special senses, such as sight, audition, olfaction and gustation. The nerves which receive these special impressions and convey them to the appropriate centres are more or less insensible to ordinary impressions. The organs to which these special nerves are distributed are generally of a complex and peculiar structure, and they present accessory parts which are important and essential in the transmission of the special impressions to the terminal branches of the nerves.

The physiological division of the nervous system into nerves and nerve-centres is carried out as regards the anatomical structure of these parts. The two great divisions of the system, anatomically considered, are into nerve-cells and nerve-fibres.

The cells of the nerve-centres, while they may transmit impressions and impulses, are the only parts capable, under any circumstances, of generating the nerve-force; and as a rule, they do not receive impressions in any other way than through the nerve-fibres. There are, however, many exceptions to this rule, as in the case of movements following direct stimulation of the sympathetic ganglia and certain centres in the brain and spinal cord; but the cells of many of the ganglia belonging to the cerebro-spinal axis are insensible to direct stimulation and can receive only impressions conducted to them by the nerves.

The nerve-fibres act only as conductors and are incapable of generating nerve-force. There is no exception to this rule, but there are differences in the properties of certain fibres. The nerves generally, for example, receive direct impressions, the motor filaments conducting these to the muscles and the sensory filaments conveying the impressions to the centres. These fibres also conduct the force generated by the nerve-centres; but there are many fibres, such as those composing the white matter of the encephalon and the spinal cord, that are insensible to direct irritation, while they convey to the centres impressions conveyed to them by sensory nerves and conduct to the motor nerves the stimulus generated by nerve-cells.

In the most natural classification of the nerve-fibres, they are divided into two groups; one embracing those fibres which have the conducting element alone, and the other presenting this anatomical element surrounded by certain accessory structures. In the course of the nerves, the simple fibres are the exception, and the other variety is the rule; but as the nerves are followed to their terminations in muscles or sensitive parts or are traced to their origin in the nerve-centres, they lose one or another of their coverings. These two varieties are designated as medullated and non-medullated fibres.

*Medullated Nerve-fibres.*—These fibres are so called because, in addition to the axis-cylinder, or conducting element, they contain, enclosed in a tubular sheath, a soft substance called medulla. This substance is strongly refractive and gives the nerves a peculiar appearance under the microscope, from which they are sometimes called dark-bordered nerve-fibres. As the whole substance of the fibre is enclosed in a tubular membrane, these are frequently called nerve-tubes.

If the nerves be examined while perfectly fresh and unchanged, their anatomical elements appear in the form of simple fibres with strongly accentuated borders. The diameter of these fibres is $\frac{1}{2500}$ to $\frac{1}{1700}$ of an inch (10 to 15 $\mu$). In a very short time the borders become darker and the fibres assume an entirely different appearance. By the use of certain reagents, it can be demonstrated that a medullated nerve-fibre is composed of three distinct portions; viz., a homogeneous sheath, a semi-fluid matter contained in the sheath, and a delicate, central band.

The tubular sheath of the nerve-fibres, the neurilemma, is a somewhat elastic, homogeneous membrane, never striated or fibrillated, and generally presenting oval nuclei with their long diameter in the direction of the tube. This is sometimes called the sheath of Schwann. In its chemical and general properties this membrane resembles the sarcolemma, although it is less elastic and resisting. It exists in all the medullated nerve-fibres, large and small, except those in the white portions of the encephalon and spinal cord. It is not certain that it does not exist in the small, non-medullated fibres, although its presence here has never been satisfactorily demonstrated.

The medullary substance fills the tube and surrounds the central band. This is called by various names, as myeline, white substance of Schwann, medullary sheath, nervous medulla etc. It does not exist either at the origin of the nerves in the gray substance of the nerve-centres or at the peripheral termination of the nerves, and it is probably not an essential conducting element. When the nerves are perfectly fresh, this substance is transparent, homogeneous, and strongly refracting, like oil; but as the nerves become altered by desiccation, the action of water, acetic acid and various other reagents, it coagulates into an opaque, granular mass. In the white substance of the encephalon and spinal cord, the neurilemma is wanting and the fibres present only the axis-cylinder surrounded with the white substance of Schwann. As a post-mortem condition, these fibres present, under the microscope, varicosities at irregular intervals, which give them a peculiar and characteristic appearance.

The medullated nerve-fibres do not have regular outlines, but present constrictions at various points in their length, called the constrictions or nodes of Ranvier. At these nodes the medullary substance is wanting and the neurilemma is in contact with the axis-cylinder. It is at these points that the transverse lines of Fromann, produced by the action of silver nitrate upon the axis-cylinder, are particularly prominent.

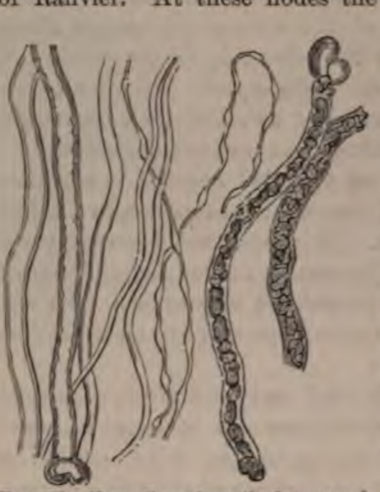


FIG. 172.—*Nerve-fibres from the human subject; magnified 350 diameters* (Kölliker).
Four small fibres of which two are varicose, one medium-sized fibre with borders of single contour, and four large fibres. Of the latter, two have a double contour, and two contain granular matter.

When a medullated nerve-fibre is slightly stretched, a number of oblique cuts are observed running across the fibre and extending to the axis-cylinder, called incisures. These involve the medullary substance only, and are best observed when this substance has been stained with osmic acid. It is not known that they possess any physiological importance.

The axis-cylinder, which occupies one-fifth to one-fourth of the diameter of the nerve-tube, is probably the conducting portion of the nerve. In the ordinary medullated fibres, the axis-cylinder can not be seen in the natural condition, because it refracts in the same manner as the medullary substance; and it can not easily be demonstrated afterward, on account of the opacity of the coagulated matter. If a fresh nerve, however, be treated with strong acetic acid, the divided ends of the fibres retract, leaving the axis-cylinder, which latter is but slightly affected by reagents. It then presents itself in the form of a pale, slightly flattened band, with outlines tolerably regular, though slightly varicose at intervals. It is somewhat granular and very finely striated in a longitudinal direction. This band is elastic but not very resisting. What serves to distinguish it from all other portions of the nerve-fibre is its insolubility in most of the reagents employed in anatomical investigations. It is slightly swollen by acetic acid but is dissolved after prolonged boiling. If nerve-tissue be treated with a solution of carmine, the axis-cylinder only is colored. It has been observed that the nerve-fibres treated with silver nitrate present in the axis-cylinder well marked, transverse striations (Fromann); and some anatomists regard both the nerve-cells and the axes of the fibres as composed of two substances, the limits of which are marked by the regular striæ thus developed. This, however, is a point of purely anatomical interest. The presence of regular and well marked striæ in the axis-cylinder after the addition of a solution of silver nitrate and the action of light can not be doubted; but it has not yet been determined whether these markings be entirely artificial or whether the axis-cylinder be really composed of two kinds of substance.

For some time it has been known that the axis-cylinders in the organs of special sense, in the final distribution of sensory nerves and in some other situations, break up into fibrillæ. A fibrillated appearance, indeed, is often observed in nerves in their course, and it is now the general opinion that the axis-cylinders are composed of fibrillæ held closely together by connective substance. This fibrillated structure of the nerves is quite prominent in some of the lower orders of animals.

The various appearances which the nerve-fibres present under different conditions are represented in Figs. 172 and 173.

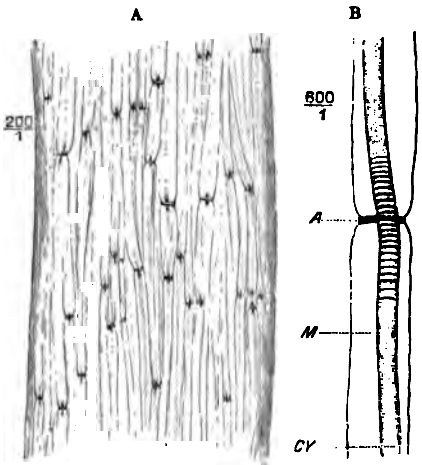



FIG. 173.—*Nodes of Ranvier and lines of Fromann* (Ranvier).

A. Intercostal nerve of the mouse, treated with silver nitrate.

B. Nerve-fibre from the sciatic nerve of a full-grown rabbit. A, node of Ranvier; M, medullary substance rendered transparent by the action of glycerine; CY, axis-cylinder presenting the lines of Fromann, which are very distinct near the node. The lines are less marked at a distance from the node.

*Non-medullated Nerve-Fibres.*—These fibres, which are largely distributed in the nervous system, appear to be simple prolongations, without alteration, of the axis-cylinders of the medullated fibres. They are found chiefly in the peripheral terminations of the nerves and in the filaments of origin of the fibres from the nerve-cells. Some anatomists think that they have a delicate investing membrane, but this has not been satisfactorily demonstrated.

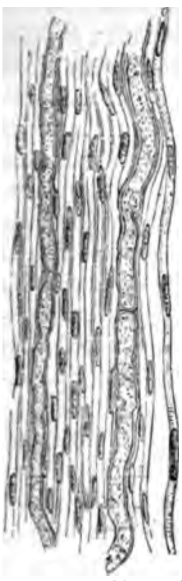


FIG. 174. — *Fibres of Remak; magnified 300 diameters* (Robin).
With the gelatinous fibres of Remak, are seen two of the ordinary, dark-bordered nerve-fibres.

*Gelatinous Nervé-Fibres* (*Fibres of Remak*).—There has been some difference of opinion with regard to the physiology of the so-called gelatinous nerve-fibres. Some anatomists have regarded them simply as elements of connective tissue, and others have described them as axis-cylinders surrounded with a nucleated sheath; but the fibres do not present the lines of Fromann when treated with silver nitrate. While elements of connective tissue may have been mistaken for true nerve-fibres, there are in the nerves, particularly in those belonging to the sympathetic system, fibres resembling the nerve-fibres of the embryon. These are the true, gelatinous nerve-fibres, or fibres of Remak. All the nerves have this structure until about the fifth month of intraüterine life, and in the regeneration of nerves after division or injury, the new elements usually assume this form before they arrive at their full development.

The true, gelatinous nerve-fibres present the following characters: They are flattened, with regular and sharp borders, grayish, pale and always fibrillated, with very fine granulations, and a number of oval, longitudinal nuclei, a characteristic which has given them the name of nucleated nerve-fibres. The diameter of the fibres is about $\frac{1}{8000}$ of an inch (3 $\mu$). The nuclei have nearly the same diameter as the fibres and are about $\frac{1}{1250}$ of an inch (20 $\mu$) in length. They are finely granular and present no nucleoli. The fibres are rendered pale by the action of acetic acid, but they are slightly swollen only, and present, in this regard, a marked contrast with the elements of connective tissue. They are found chiefly in the sympathetic system and in that particular portion of this system connected with involuntary movements. They are not usually found in the white filaments of the sympathetic.

*Accessory Anatomical Elements of the Nerves.*—The nerves present, in addition to the different varieties of true nerve-fibres just described, certain accessory anatomical elements common to nearly all of the tissues of the organism, such as connective tissue, blood-vessels and lymphatics.

Like the muscular tissue, the nerves are made up of their true anatomical elements—the nerve-fibres—held together into primitive, secondary and tertiary bundles, and so on, in proportion to the size of the nerve. The primitive fasciculi are surrounded with a delicate membrane, described by Robin, under the name of *périnèvre*, but which had been already noted by other anatomists, under different names, and is now frequently called the sheath of Henle. This membrane is homogeneous or very finely granular, sometimes marked with longitudinal striæ, and possessing elongated, granular nuclei. According to Ranvier, there are three kinds of nuclei either attached to or situated near the sheath. These are (1) nuclei attached to the inner surface of the sheath; (2) nuclei belonging to the nerve-fibres within the sheath; and (3) nuclei of connective-tissue elements near the sheath. Treated with silver nitrate, the sheath presents the borders of a lining endothelium. The sheath of Henle begins at the point where the nerve-fibres emerge from the white portion of the nervous centres, and it extends to their terminal extremities, being interrupted by the ganglia in the course of the nerves. This membrane generally envelops a primitive fasciculus of fibres, branching as the bundles divide and pass from one trunk to another, and is sometimes found surrounding single fibres. It usually is not penetrated by blood-vessels, the smallest capillaries of the nerves ramifying in its substance but seldom passing through to the individual nerve-fibres. Within the sheath of Henle are sometimes found elements of connective tissue, with very rarely a few capillary blood-vessels in the largest fasciculi.

The quantity of fibrous tissue in the different nerves is very variable and depends upon the conditions to which they are subjected. In the nerves within the bony cavities, where they are entirely protected, the fibrous tissue is very scanty; but in the nerves between muscles, there is a tolerably strong investing membrane or sheath surrounding the whole nerve and sending into its interior processes which envelop smaller bundles of fibres. This sheath is formed of ordinary fibrous tissue, with small elastic fibres and nucleated connective-tissue cells. These latter may be distinguished from the gelatinous nerve-fibres by the action of acetic acid, which swells and finally dissolves them, while the nerve-fibres are but slightly affected.

The greatest part of the fibrous sheath of the nerves is composed of bundles of white inelastic tissue, interlacing in every direction; but it contains also many elastic fibres, adipose tissue, a net-work of arteries and veins, and "nervi nervorum," which are to these structures what the vasa vasorum are to the blood-vessels. The adipose tissue is constant, being found even in extremely emaciated persons (Sappey).

The vascular supply to most of the nerves is rather scanty. The arteries break up into a plexus of very fine capillaries, arranged in oblong, longitudinal meshes surrounding the fasciculi of fibres; but they rarely penetrate the sheath of Henle, and they do not usually come in contact with the ultimate nervous elements. The veins are rather more voluminous and follow the arrangement of the arteries. Lymph-spaces, lined by delicate endothelium, are found in the connective-tissue sheaths of the bundles of fibres.

*Branching and Course of the Nerves.*—The ultimate nerve-fibres in the course of the nerves have no connection with each other by branching or inosculation. A bundle of fibres frequently sends branches to other nerves and receives branches in the same way; but this is simply the passage of fibres from one sheath to another, the ultimate fibres themselves maintaining throughout their course their individual physiological properties. The nerve-fibres do not branch or inosculate except near their termination. When there is branching of medullated fibres, it is always at the site of one of the nodes of Ranvier. The branching and inosculation of the ultimate nerve-fibres will be fully described in connection with their final distribution to muscles and sensitive parts.

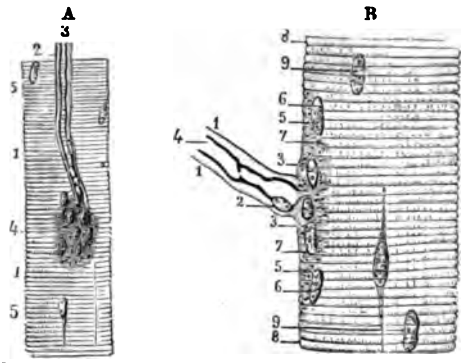



FIG. 175.—*Mode of termination of the motor nerves* (Rouget).

A, primitive fasciculus of the thyro-hyoid muscle of the human subject, and its nerve-tube: 1, 1, primitive muscular fasciculus; 2, nerve-tube; 3, medullary substance of the tube, which is seen extending to the terminal plate, where it disappears; 4, terminal plate situated beneath the sarcolemma, that is to say, between it and the elementary fibrillæ; 5, 5, sarcolemma.

B, primitive fasciculus of the intercostal muscle of the lizard, in which a nerve-tube terminates: 1, 1, sheath of the nerve-tube; 2, nucleus of the sheath; 3, 3, sarcolemma becoming continuous with the sheath; 4, medullary substance of the nerve-tube, ceasing abruptly at the site of the terminal plate; 5, 5, terminal plate; 6, 6, nuclei of the plate; 7, 7, granular substance which forms the principal element of the terminal plate and which is continuous with the axis-cylinder; 8, 8, undulations of the sarcolemma reproducing those of the fibrillæ; 9, 9, nuclei of the sarcolemma.

*Termination of Nerves in Voluntary Muscles.*—The mode of termination of motor nerves in voluntary muscles was indicated by Doyère, in 1840, was quite fully described by Rouget, in 1862, and has since been studied by anatomists, who have extended and elaborated these researches. It is the general opinion that but one nerve-ending exists in each muscular fibre in the mammalia, while several exist in cold-blooded animals. In man and in the warm-blooded animals generally, the medullated nerve-fibres divide dichotomously near their endings in the muscular fibres, each division always taking place at a node of Ranvier. The fibres finally resulting from these divisions pass to the sarcolemma and terminate in a rather prominent mass called an end-plate, with six to twelve or sometimes sixteen nuclei which are distinct from the nuclei of the muscular fibre. The tubular membrane of the nerve-fibre here fuses with the sarcolemma (Rouget) and the medullary substance is lost. By the action of gold chloride, it has been shown that fibrils arise from the under surface of the end-plates, which pass into the substance of the muscular fibres, between the muscular fibrillæ.

FIG. 176.—*Intrafibrillar terminations of a motor nerve in striated muscle, stained with gold chloride* (Landois).

These fibrils probably are connected with the axis-cylinders, but their exact mode of termination in the muscular substance has not been satisfactorily demonstrated.

Although the sensibility of the muscles is slight as compared with that of the skin and mucous membranes, they are not insensible and they possess nerve-fibres other than those exclusively motor. According to Kölliker, small medullated fibres go to the muscular tissue and here give off very fine non-medullated fibres, which terminate in fibres of the same appearance but provided with nuclei. These form a plexus on the sarcolemma and surround the muscular fibres. It is not certain that they penetrate the sarcolemma and terminate in the muscular substance, although this view has been advanced.


FIG. 177.—*Termination of nerves in non-striated muscle* (Cadiat).

*Termination of Nerves in the Involuntary Muscular Tissue.*—According to the observations of Frakenhaeuser upon the nerves of the uterus, the nerve-fibres form a plexus in the connective tissue surrounding the involuntary muscles and then send small fibres into the sheets or layers of muscular-fibre cells, which branch and finally go into the nucleoli of these structures. Arnold has confirmed these observations and has shown farther that in many instances, the fine, terminal nerve-fibres branch and go into the nuclei of the muscular fibres and afterward pass out to join with other fibres and form a plexus.

*Termination of the Nerves in Glands.*—The researches of Pflüger upon the salivary glands leave no doubt of the fact that medullated nerve-fibres pass to the cells of these organs and there abruptly terminate, at least as dark-bordered fibres. This author believes, however, that having formed a more or less branching plexus, non-medullated fibres pass directly into the glandular cells and terminate in the nucleoli. The same observer has described and figured multipolar cells, mixed with the glandular cells, in which some of the nerve-fibres terminate. These, however, are not found in the parotid. These nerve-fibres are regarded as glandular nerves, and they are distinct from the vaso-motor nerves.

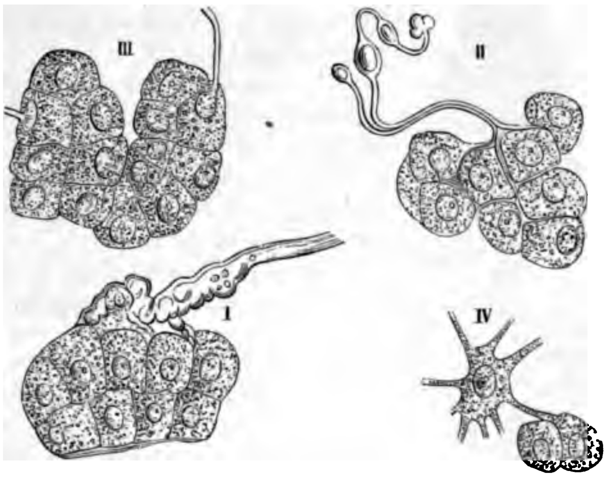



**FIG. 178.**—*Termination of the nerves in the salivary glands* (Pflüger). I, II, branching of the nerves between the glandular cells; III, terminations of the nerves in the nuclei of the cells; IV, multipolar nerve-cell.

*Modes of Termination of the Sensory Nerves.*—There undoubtedly are several modes of termination of the sensory nerves in integument and in mucous membranes, some of which have been quite accurately described, while others are still somewhat uncertain. In the first place, anatomists now recognize three varieties of corpuscular terminations, differing in their structure, probably, according to the different properties connected with sensation, with which the parts are endowed. In addition it is probable that sensory nerves are connected with the hair-follicles, which are so largely distributed throughout the cutaneous surface. There are, also, terminal filaments not connected with any special organs, some of them, perhaps, ending simply in free extremities, and some connected with epithelium. There are still differences of opinion concerning these various modes of termination of the nerves, but with regard to the terminal corpuscles, these differences relate mainly to anatomical points. It is not proposed, therefore, to enter fully into the discussions upon these questions, but simply to present what seem to be the most reliable anatomical views.

*Corpuscles of Vater or of Pacini.*—These bodies were called corpuscles of Pacini, until it was shown that they had been seen about a century and a half ago by Vater. In man, they are oval or egg-shaped and measure $\frac{1}{25}$ to $\frac{1}{6}$ of an inch (1 to 4 mm.) in length. They are always found in the subcutaneous layer on the palms of the hands and the soles of the feet, and are most abundant on the palmar surfaces of the fingers and toes, particularly the third phalanges. In the entire hand there are about six hundred, and about the same number on the feet. They are sometimes, but not constantly, found in the following situations: the dorsal surfaces of the hands and feet, on the cutaneous nerves of the arm, the forearm and the neck, the internal pudic nerve, the intercostal nerves, all of the articular nerves of the extremities, the nerves beneath the mammary glands, the nerves of the nipples, and in the substance of the muscles of the hands and feet. They are found without exception on all of the great plexuses of the sympathetic system, in front of and by the sides of the abdominal aorta, and behind the peritoneum, particularly in the vicinity of the pancreas. They sometimes exist in the mesentery and have been observed near the coccygeal gland.

FIG. 179. — *Corpuscle of Vater* (Sappey).

1, base of the corpuscle; 2, apex; 3, 3, 3, substance of the corpuscle, in layers; 4, 4, nerve penetrating the corpuscle; 5, cavity of the corpuscle; 6, nerve; 7, nerve, which has lost its medullary substance and sheath; 8, termination of the nerve; 9, granular substance continuous with the nerve.

The corpuscles consist simply of several layers of connective tissue enclosing one, two or three central bulbs in which are found the ends of the nerve. These bulbs are finely granular and nucleated, and are regarded by most anatomists as composed of connective tissue. At the base of the corpuscle, is a pedicle formed of connective tissue surrounding a medullated nerve-fibre which penetrates the corpuscle. Within the corpuscle the medullary substance of the nerve-fibre is lost and only the axis-cylinder remains.

The situation of these corpuscles, beneath the true skin instead of in its substance, shows that they can not be properly considered as tactile corpuscles, a name which is applied to other structures found in the papillæ of the corium; and it is impossible to assign to them any special use connected with sensation, such as the appreciation of temperature, pressure or weight. All that can be said with regard to them is that they constitute one of the several modes of termination of the nerves of general sensibility.

*Tactile Corpuscles.*—The name tactile corpuscles implies that these bodies are connected with the sense of touch; and this view is sustained by the fact that they are found almost exclusively in parts endowed to a marked degree with tactile sensibility. They are sometimes called the corpuscles of Meissner and Wagner, after the anatomists by whom they were first described. The true, tactile corpuscles are found in greatest number on the palmar surfaces of the hands and fingers and the plantar surfaces of the feet and toes. They exist, also, in the skin on the backs of the hands and feet, the nipples, and a few on the anterior surface of the forearm. The largest papillæ of the skin are found on the hands, feet and nipples, precisely where the tactile corpuscles are most abundant. Corpuscles do not exist in all papillæ, and they are found chiefly in those called compound. In an area a little more than $\frac{1}{12}$ of an inch square (2·2 mm. square), on the third phalanx of the index-finger, Meissner counted four hundred papillæ, in one hundred and eight of which he found tactile corpuscles, or about one in four. In an equal area on the second phalanx, he found forty corpuscles; on the first phalanx, fifteen; eight on the skin of the hypothenar eminence; thirty-four on the plantar surface of the ungual phalanx of the great-toe; and seven or eight in the skin on the middle of the sole of the foot. In the skin of the fore-arm the corpuscles are very rare. According to Kölliker, the tactile corpuscles

FIG. 180.—*Papillæ of the skin of the palm of the hand* (Sappey).
1, papilla with two vascular loops; 2, papilla with a tactile corpuscle; 3, papilla with three vascular loops; 4, 5, large, compound papillæ; 6, 6, vascular net-work beneath the papillæ; 7, 7, 7, 7, vascular loops in the papillæ; 8, 8, 8, 8, nerves beneath the papillæ; 9, 9, 10, 11, tactile corpuscles.

usually occupy special papillæ which are not provided with blood-vessels; so that the papillæ of the hand may be properly divided into vascular and nervous.

The form of the tactile corpuscles is oblong, with their long diameter in the direction of the papillæ, Their length is $\frac{1}{350}$ to $\frac{1}{250}$ of an inch (66 to 100 $\mu$). In the palm of the hand they are $\frac{1}{250}$ to $\frac{1}{140}$ of an inch (100 to 165 $\mu$) long, and $\frac{1}{560}$ to $\frac{1}{500}$ of an inch (45 to 50 $\mu$) in thickness. They generally are situated at the summits of the secondary eminences of the compound papillæ. They consist of a central bulb of homogeneous or slightly-granular connective-tissue substance, harder than the central bulb of the corpuscles of Vater, and a covering. The covering is composed of connective tissue with a few fine elastic fibres. One, two, and sometimes three or four dark-bordered nerve-fibres pass from the subcutaneous nervous plexus to the base of each corpuscle. These surround the corpuscle with two or three spiral turns, and they terminate by pale extremities on the surface of the central bulb.

*End-Bulbs.*—Under this name, a variety of corpuscles has been described by Krause, as existing in the conjunctiva covering the eye and in the semilunar fold, in the floor of the buccal cavity, the tongue, the glans penis and the clitoris. They bear some analogy to the tactile corpuscles, but they are much smaller and more simple in their structure. They form rounded or oblong enlargements at the ends of the nerves, which are composed of homogeneous matter with a delicate investment of connective tissue. They measure $\frac{1}{1000}$ to $\frac{1}{250}$ of an inch (25 to 100 $\mu$) in diameter. In the parts provided with papillæ, they are situated at the summits of the secondary elevations. The arrangement of the nerve-fibres in these corpuscles is very simple. One, two, or three medullated fibres pass from the submucous plexus to the corpuscles. The investing sheath of the fibres is here continuous with the connective-tissue covering of the corpuscle, and the nerve-fibres pass into the corpuscle, break up into two or three divisions, and terminate in convoluted or knotted coils. The nerve-fibres are medullated for a certain distance, but their terminations are generally pale. The above is one form of these corpuscles. Sometimes, however, the terminal bulbs are oblong, and sometimes but a single nerve-fibre penetrates the bulb and terminates in a simple, pale filament. The principal forms of the terminal bulbs are shown in Fig. 181.

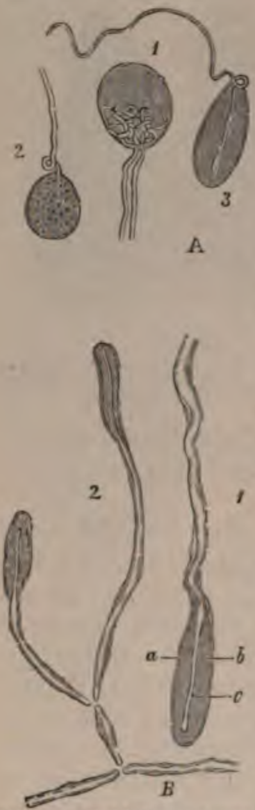


FIG. 181.—*End-bulbs, or corpuscles of Krause* (Ludden).

A, three corpuscles of Krause from the conjunctiva of man, treated with acetic acid; magnified 300 diameters: 1, spherical corpuscle, with two nerve-fibres which form a knot in its interior (portions of two pale nerve-fibres are also seen); 2, a rounded corpuscle presenting a nerve-fibre and fatty granulations in the internal bulb; 3, an elongated corpuscle with a distinct terminal fibre.

In these three corpuscles, the covering, nucleated in 1 and 2, is distinguished.

B, terminal bulbs from the conjunctiva of the calf, treated with acetic acid; magnified 300 diameters: 1, extremity of a nerve-fibre with its bulb; 2, double bifurcation of a nerve-fibre, with two terminal bulbs; *a*, covering of the terminal bulbs; *b*, internal bulb; *c*, pale nerve-fibre.

*General Mode of Termination of the Sensory Nerves.*—The actual termination of the sensory nerves upon the general surface and in mucous membranes is still a question of some obscurity. Although anatomists have arrived at a pretty definite knowledge of the sensory corpuscles, it must be remembered that there is an immense cutaneous and mucous surface in which no corpuscles have as yet been demonstrated; and it is in these parts, endowed with what may be called general sensibility, as distinguished from the sense of touch, that the mode of termination of the nerves remains to be studied.

According to Kölliker, in the immense majority of instances the sensory nerves terminate in some way in the hair-follicles. If this be true, it will account for the termination of the nerves in by far the greatest portion of the skin, as there are few parts in which hair-follicles do not exist; but unfortunately the exact mode of connection of the nerves with these follicles is not apparent. The following seems to be all that is positively known of the terminations of the nerves on the general surface:

Medullated nerve-fibres form a plexus in the deeper layers of the true skin, and from this plexus, fibres, some pale and nucleated and others medullated, pass to the hair-follicles, divide into branches, penetrate into their interior and are there lost. A certain number of fibres pass to the non-striated muscular fibres of the skin. A certain number pass to papillæ and terminate in tactile corpuscles, and others pass to papillæ that have no tactile corpuscles.

In the mucous membranes the mode of termination is, in general terms, by a delicate plexus just beneath the epithelium, coming from a submucous plexus analogous to the deep cutaneous plexus. In certain membranes the nerves terminate in end-bulbs, or corpuscles of Krause. In the cornea, according to the observations of Hoyer, Lipmann and others, branching nerve-fibres pass to the nucleoli of the corneal corpuscles and to the nucleoli of the cells of the posterior layer of epithelium.

*Structure of the Nerve-centres.*—A peculiar pigmentary matter in the nerve-cells and in the surrounding granular substance gives to the nerve-centres a grayish color, by which they are readily distinguished from the white, or fibrous division of the nervous system. Wherever this gray matter is found, the anatomical elements of the tissue are cellular, except in the nerves formed of gray, or gelatinous fibres. Under the general division of nerve-centres, are included, anatomically at least, the gray matter of the cerebro-spinal centres, the ganglia of the roots of the spinal and certain of the cranial nerves, and the ganglia of the sympathetic system. In these parts are found cells, which constitute the essential anatomical element of the tissue, granular matter resembling the contents of the cells, pale fibres originating in prolongations of the cells, elements of connective tissue, delicate membranes enveloping some of the cells, with blood-vessels and lymphatics. The most important of these structures, in their physiological relations, are the cells and the prolongations by which they are connected with the nerves and with each other.


FIG. 182.—*Unipolar cell from the Gasserian ganglion* (Schwalbe). N, N, N, nuclei of the sheath ; T, fibre branching at a node of Ranvier.

*Nerve-cells.*—The following varieties of cells exist in the nerve-centres and constitute their essential anatomical elements ; viz., unipolar, bipolar and multipolar cells. These cells present great differences in their size and general appearance, and some distinct varieties are found in particular portions of the nervous system. Unipolar and bipolar cells are found in the ganglia of the cranial nerves and in the ganglia of the posterior roots of the spinal nerves. Small unipolar cells are found in the sympathetic ganglia. Multipolar cells present three or more prolongations. Small cells, with three and rarely four prolongations, are found in the posterior cornua of the gray matter of the spinal cord. From their situation they have been called sensory cells. They are found in greatest number in parts known to be endowed exclusively with sensory properties. Large, irregularly shaped multipolar cells, with a number of poles, or prolongations, are found chiefly in the anterior cornua of the gray matter of the spinal cord, and these have been called motor cells. They sometimes present as many as ten or twelve poles.

Unipolar cells, such as exist in the ganglia of the nerves as distinguished from the ganglia of the cerebro-spinal axis, have but a single prolongation, which is continuous with a nerve-fibre. These cells frequently have a connective-tissue envelope, or sheath, which is prolonged as a sheath for the nerve. Unipolar cells, with a connective-tissue sheath, the pole being surrounded by a spiral fibre, have been observed in the sympathetic ganglia of the frog. These do not exist in the human subject or in the mammalia and nothing is known of the uses of the spiral fibres.

FIG. 183.—*Unipolar nerve-cell with a spiral fibre* (Landois).

FIG. 184.—*Bipolar nerve-cell* (Landois).

Bipolar cells seem to be nucleated enlargements in the course of medullated nerve-fibres. Usually the medullary substance does not extend over the cell, although this sometimes occurs.

Multipolar cells have a number of poles, but there is always one pole which does not branch and which becomes continuous with the axis-cylinder of a nerve-fibre. This is called the axis-cylinder prolongation. Of the other poles, some are continuous with poles of contiguous cells, connecting numbers of cells into groups, and others, which are sometimes called protoplasmic prolongations, branch freely and are lost in the intercellular substance.


FIG. 185.—*Multipolar nerve-cell from the spinal cord* (Landois). Z, axis-cylinder prolongation; Y, protoplasmic branches.

With all the differences in the size and form of the nerve-cells, they present tolerably uniform general characters as regards their structure and contents. With the exception of the unipolar and bipolar cells, they are irregular in shape, with strongly refracting, granular contents, frequently a considerable number of pigmentary granules, and always a distinct nucleus and nucleolus. The nucleus in the adult is almost invariably single, although, in rare instances, two have been observed. Cells with multiple nuclei are often observed in young animals. The nucleoli usually are single, but there may be as many as four or five. The diameter of the cells is variable. They usually measure $\frac{1}{1250}$ to $\frac{1}{500}$ of an inch (20 to 50 $\mu$); but there are many of larger size and some are smaller. The nuclei measure $\frac{1}{2000}$ to $\frac{1}{1250}$ of an inch (12 to 20 $\mu$.) The nerve-cells are soft, have no true cell-membrane and are fibrillated, the fibrillation extending to the poles. The transverse striæ in the axis-cylinder treated with silver nitrate, noted by Fromann and confirmed by Grandry and others, have been observed by Grandry in the substance of the nerve-cells. While this fact, perhaps, shows that the substance contained in the cells and their prolongations is like the substance of the axis-cylinder, it is possible that the

FIG. 186.—*Transverse section of the gray substance of anterior cornua of the spinal cord of the ox, treated with silver nitrate* (Grandry).

markings may be entirely artificial, and that they do not indicate the existence of two distinct substances.

Tracing the nerve-fibres toward their origin, they are seen to lose their investing membrane as they pass into the white portion of the centres, being here composed only of medullary substance surrounding the axis-cylinders. They then penetrate the gray substance, in the form of axis-cylinders, losing the medullary substance. In the gray substance, it is impossible to make out all their relations distinctly, and it can not be stated, as a matter of positive demonstration, that all of them are connected with the poles of nerve-cells. Still, it has been shown in the gray matter of the spinal cord, that many of the fibres are actual prolongations of the cells, others probably passing upward to be connected with cells in the encephalon.

Tracing the prolongations from the cells, it is found that at least one of the poles in the gray substance gives origin to nerve-fibres, but that these fibres do not branch after they pass into the white substance. Other poles connect the nerve-cells with each other by commissural fibres of greater or less length; and it is probable that the cells are thus arranged in separate and distinct groups, possibly connected with sets of muscles.

*Accessory Anatomical Elements of the Nerve-centres.*—In addition to the cells of the gray matter and the axis-cylinder of the nerves, which are probably the only structures directly concerned in innervation, are the following accessory anatomical elements: 1, outer coverings surrounding some of the cells; 2, intercellular, granular matter; 3, peculiar corpuscles, called myelocytes; 4, connective-tissue elements; 5, blood-vessels and lymphatics.

Certain of the cells in the spinal ganglia and in the ganglia of the sympathetic system are surrounded with a covering, removed a certain distance from the cell itself so as to be nearly twice the diameter of the cell, which is continuous with the sheath of the dark-bordered fibres. This membrane is always nucleated and is composed of a layer of very delicate endothelium. Its physiological significance is not apparent.

In the gray matter of the nerve-centres, there is a finely granular substance between the cells, which closely resembles the granular contents of the cells themselves. In addition to this granular matter, Robin has described peculiar anatomical elements which he called myelocytes. These are found in the cerebro-spinal centres, forming a layer near the boundary of the white substance, and they are particularly abundant in the cerebellum. They exist in the form of free nuclei and nucleated cells, the free nuclei being by far the more abundant. The nuclei are rounded or ovoid, with strongly accentuated borders, are unaffected by acetic acid, finely granular and generally without nucleoli. The cells are rounded or slightly polyhedric, pale, clear or very slightly granular, and contain bodies similar to the free nuclei. The free nuclei are $\frac{1}{5000}$ to $\frac{1}{4000}$ of an inch (5 to 6 $\mu$) in diameter, and the cells measure $\frac{1}{2500}$ to $\frac{1}{2000}$, and sometimes $\frac{1}{1500}$ of an inch (10, 12 and 15 $\mu$). These elements also exist in the second layer of the retina.

In the cerebro-spinal centres there is a delicate stroma of connective tissue, chiefly in the form of stellate, branching cells, which serves in a measure, to support the nervous elements. This tissue, which is peculiar to the white substance of the encephalon and spinal cord, is called neuroglia.

The blood-vessels of the nerve-centres form a capillary net-work with large meshes. The gray substance is richer in capillaries than the white.

A peculiarity of the vascular arrangement in the cerebro-spinal centres has already been described in connection with the anatomy of the lymphatic system. The blood-vessels here are surrounded by what have been called perivascular canals, first described by Robin and afterward shown by His and Robin to be radicles of the lymphatic system.

*Composition of the Nervous Substance.*—The chemistry of the nervous substance, as far as it is understood, throws little light on its physiology. Certain albuminoids have been extracted which do not possess more than a purely chemical interest. The substance called cerebrine is composed of carbon, hydrogen, oxygen and nitrogen, without either sulphur or phosphorus. Protagon is a nitrogenized substance containing phosphorus (Liebreich, 1865). By some chemists protagon is thought to be a mixture of cerebrine and lecethine. Lecethine is regarded as a nitrogenous fat. Other substances which have been extracted—xanthine, hypoxanthine, inosite, creatine and various volatile fatty acids—have no special physiological interest connected with the nervous system and are found in many other situations. Cholesterine, which always exists in considerable quantity in the nervous tissue, has been considered in connection with the physiology of excretion. The ordinary fats are in combination with other fats or with peculiar acid substances. The reaction of nerve-tissue is either neutral or faintly alkaline under normal conditions, soon becoming acid after death.

*Degeneration and Regeneration of Nerves.*—The degenerations observed in nerves separated from the centres to which they are normally attached, first studied by Waller, in 1850, are now used in following out certain nervous connections too intricate to be revealed by ordinary dissection. This is known as the Wallerian method. If an ordinary mixed nerve be divided in its course, both the motor and sensory fibres of the peripheral portion undergo fatty degeneration and lose their excitability. As regards the spinal nerves, degeneration occurs in the motor fibres only, when the anterior spinal root has been divided, and the nerve has degenerated fibres (motor) mixed with the sensory fibres, which latter retain their anatomical and physiological characters. The motor fibres of the spinal nerves are degenerated when separated from their connections with the anterior cornua of gray matter of the cord. If the posterior roots of the spinal nerves be divided beyond the ganglia, the peripheral sensory fibres degenerate; but if the ganglia be exsected, the central as well as the peripheral portions degenerate. These experiments show the existence of centres which preside over the nutrition of the nerves. The centres for the motor filaments of the spinal nerves are in the anterior cornua of gray matter of the cord. The centres for the sensory fibres are the ganglia of the posterior roots. The centres for the sensory cranial nerves are the ganglia on their roots; and the centres for the motor cranial nerves are probably the gray nuclei of origin of these nerves. The Wallerian method has been found useful in studying the paths of conduction in the encephalon and spinal cord, as will be seen in connection with the physiology of these parts.

The excitability of the motor nerves disappears in about four days after their section. Of course, in experiments upon this point, it is necessary to excise a portion of the nerve to prevent reunion of the divided extremities; but when this is done, after about the fourth day, stimulation of the nerve will produce no contraction in the muscles, although the latter retain their contractility. This loss of excitability is gradual, and it continues, whether the nerve be exposed and stimulated from time to time or be left to itself, progressing from the centres to the periphery. In the researches of Longet upon this subject, it was found that the lower portion of the peduncles of the brain lost their excitability first, then the anterior columns of the cord, then the motor roots of the nerves, and last of all, the branches of the nerves near their terminations in the muscles.

The sensibility of the sensory nerves disappears from the periphery to the centres, as is shown in dying animals and in experiments with anæsthetics. The sensibility is lost, first in the terminal branches of the nerves, next in the trunks and in the posterior roots of the spinal nerves, and so on to the centres.

Nerves that have been divided may be regenerated if anatomical union of the divided ends can be obtained; and this sometimes takes place several months after injury to the nerves, the regeneration occurring by the formation of new fibres. Mixed nerves are regenerated in this way, and conduction is finally restored in both directions. The sensory conduction appears first, and next, the conduction of motor impulses. The restoration of the physiological properties of the nerves occupies several weeks. The central end of a mixed nerve has been made to unite with the peripheral end of another mixed nerve, but it is doubtful whether a divided end of a motor nerve is ever united to the divided end of a sensory nerve. Experiments upon this latter point are not entirely satisfactory.

### Motor and Sensory Nerves.

Aside from the nerves possessing special properties, such as the nerves of sight, hearing, smell, taste and, according to some physiologists, nerves of touch, temperature, sense of weight and muscular sense, the cerebro-spinal nerves present two kinds of fibres. These are (1) centrifugal, or motor fibres, and (2) centripetal, or sensory fibres. The motor fibres conduct impulses from the centres to the muscles and excite muscular action. The sensory fibres conduct impressions from the periphery to the centres, which are appreciated either as ordinary sensation or as pain. As regards the nerves arising by two roots from the spinal cord, the exact anatomical and physiological divisions into motor and sensory were first made by Magendie, in 1822. As will be seen farther on, this division is distinct for the cranial nerves, so that it is universal in the cerebro-spinal system. The importance of the discovery of the distinct properties of the two roots of the spinal nerves is such that it merits at least a brief historical account, particularly as this discovery is quite generally attributed to Charles Bell.

The first definite statement with regard to distinct properties of the two roots of the spinal nerves was made by Alexander Walker, in 1809, who said that the posterior roots were for motion and the anterior roots for sensation, the exact reverse of the truth.

In a pamphlet privately printed by Charles Bell, probably in 1811, and "submitted for the observations of his friends," the view was advanced that the anterior roots are both motor and sensory and that the posterior preside over "the secret operations of the bodily frame, or the connections which unite the parts of the body into a system."

In 1822, Magendie, as the result of experiments upon the exposed roots in living dogs, stated that "he was able at that time to advance as positive, that the anterior and the posterior roots of the nerves which arise from the spinal cord have different functions, that the posterior seem more particularly destined to sensibility, while the anterior seem more specially connected with motion."

It is now universally admitted that the mixed nerves arising from the spinal cord derive their motor properties from the anterior roots and their sensory properties from the posterior roots.

The anterior roots possess a certain degree of sensibility in addition to their motor properties (Magendie). This sensibilitity, which is slight, is derived from fibres from the posterior roots, which turn back to go to the anterior roots. This fact has been positively demonstrated by the Wallerian method. When a posterior root is divided beyond the ganglion, the sensibility of the corresponding anterior root is lost, and degenerated fibres appear, after a few days, in the anterior roots (Schiff). This sensibility of the anterior roots is called recurrent sensibility. Similar relations are observed between certain of the motor and sensory cranial nerves.

*Mode of Action of the Motor Nerves.*—As regards the normal action of the motor nerves, a force, the nature of which is unknown, generated in the centres, is conducted from the centres to the peripheral distribution of the nerves in the muscles, and is here manifested by contraction. Their mode of action, therefore, is centrifugal. When these motor filaments are divided, the connection between the parts animated by them and the centre is interrupted, and motion in these parts, in obedience to the natural stimulus, becomes impossible. While, however, it is not always possible to induce generation of nerve-force in the centres by the direct application of any agent to them, this force may be imitated by stimulation applied to the nerve itself. A nerve that will thus respond to direct stimulation is said to be excitable.

If a motor nerve be divided, electric, mechanical, or other stimulus applied to the extremity connected with the centres produces no effect; but the same stimulus applied to the extremity connected with the muscles is followed by contraction. The phenomena indicating that a nerve retains its physiological properties are always manifested at its peripheral distribution, and these do not essentially vary when the nerve is stimulated at different points in its course. For example, stimulation of the anterior roots near the cord produces contraction in those muscles to which the fibres of these roots are distributed; but the same effect follows stimulation of the nerve going to these muscles, in any part of its course.

As far as their physiological action is concerned, the individual nerve-fibres are entirely independent; and the relations which they bear to each other in nervous fasciculi and in the so-called anastomoses of nerves involve simple contiguity. Comparing the nerve-force to galvanism, each individual fibre seems completely insulated; and a stimulus conducted by it to muscles never extends to the adjacent fibres. That it is the axis-cylinder which conducts and the medullary tube which insulates, it is impossible to say with positiveness; but it is more than probable that the axis-cylinder is the only conducting element.

The generation of a motor impulse may be induced by an impression made upon sensory nerves and conveyed by them to the centres. If, for example, a certain portion of the central nervous system, as the spinal cord, be isolated, leaving its connections with the motor and sensory nerves intact, these phenomena may be readily observed. An impression made upon the sensory nerves will be conveyed to the gray matter of the cord and will induce the generation of a motor impulse by the cells of this part, which will be conducted to the muscles and give rise to contraction. As the impulse, in such observations, seems to be reflected from the cord, through the motor nerves, to the muscles, this action has been called reflex. These phenomena constitute an important division of the physiology of the nervous system and will be fully considered by themselves.

*Associated Movements.*—It is well known that the action of certain muscles is with difficulty isolated by an effort of the will. This applies to sets of muscles upon one side of the body and to corresponding muscles upon the two sides. For example, it is almost impossible, without great practice, to move some of the fingers, at the same time restraining the movements of the others; and the action of certain sets of muscles of the extremities is always simultaneous. The toes, which are but little used as the foot is confined in the ordinary dress, are capable of very little independent action. It is difficult to move one eye without the other, or to make rapid rotary movements of one hand while an entirely different order of movements is executed by the other; and instances of this kind might be multiplied. In studying these associated movements, the question arises as to how far they are due to the anatomical relations of the nerves to the centres and their connections with muscles, and how far they depend upon habit and exercise. There may be certain sets of nerve-cells connected with each other by commissural fibres and giving origin to motor nerves distributed to sets of muscles, an anatomical arrangement that might render a separate action of these cells impossible. The anatomy of the nerve-centres and their connection with fibres are so difficult of investigation, that demonstrative proof of the existence of such systems is impracticable; but this would afford a ready explanation of the fact that it is impossible, as a rule, by an effort of the will, to cause only a portion of a single muscle to contract; yet some of the larger muscles receive a considerable number of motor nerve-fibres which are probably connected with gray matter composed of many anastomosing nerve-cells.

Many of the associated movements may be influenced to a remarkable degree by education, of which no better example can be found than in the case of skillful performers upon certain musical instruments, such as the piano, harp, violin and other stringed instruments. In the technical study of such instruments, not only does one hand become almost independent of the other, but very complex associated movements may be acquired. An accomplished pianist or violinist executes the different scales automatically by a single effort of the will, and pianists frequently execute at the same time scales with both hands, the action being entirely opposed to the natural association of movements.

Looking at the associated movements in their relations to the mode of action of the motor nerves, it seems probable that as a rule, the anatomical relations of the nerves are such that a motor impulse or an effort of the will can not be conducted to a portion only of a muscle, but must act upon the whole muscle, and the same is true, probably, of certain restricted sets of muscles; but the association of movements of corresponding muscles upon the two sides of the body, with the exception, perhaps, of the muscles of the eyes, is due mainly to habit and may be greatly modified by education.

*Mode of Action of the Sensory Nerves.*—The sensory nerve-fibres, like the fibres of the motor nerves, are entirely independent of each other in their action; and in the so-called anastomoses that take place between sensory nerves, the fibres assume no new relations, except as regards contiguity.

As motor fibres convey to their peripheral distribution the impulse produced by a stimulus applied in any portion of their course, so an impression made upon a sensory nerve is always referred to the periphery. A familiar example of this is afforded by the very common accident of contusion of the ulnar nerve as it passes between the olecranon and the condyle of the humerus. This is attended with painful tingling of the ring and little finger and other parts to which the filaments of this nerve are distributed, without, necessarily, any pain at the point of injury. More striking examples are afforded in neuralgic affections dependent upon disease of or pressure upon the trunk of a sensory nerve. In such cases, excision of the nerve is often practised, but no permanent relief follows unless the section be made between the affected portion of the nerve and the nerve-centres; and the pain is always referred to the termination of the nerve, even after it has been divided between the seat of the disease and the periphery, leaving the parts supplied by the nerve insensible to direct irritation. In cases of disease it is not unusual to note great pain in parts of the skin that are insensible to direct impressions. The explanation of this is that the nerves are paralyzed near their terminal distribution, so that an impression made upon the skin can not be conveyed to the sensorium; but the trunks of the nerves still retain their conducting power and are the seat of diseased action, producing pain which is referred by the patient to the periphery. In the very common operation of restoring the nose by transplanting skin from the forehead, after the operation has been completed, the skin having been entirely separated, and united in its new relations, the patient feels that the forehead is touched when the finger is applied to the artificial nose. After a time, however, the sensorium becomes accustomed to the new arrangement of the parts, and this deceptive feeling disappears.

There are certain curious nervous phenomena, that are not without physiological interest, presented in persons who have suffered amputations. It has long been observed that after loss of a limb, the sensation of the part remains; and pain is frequently experienced, which is referred to the amputated member. Thus a patient will feel distinctly the fingers or toes after an arm or a leg has been removed, and irritation of the ends of the nerves at the stump produces sensations referred to the missing member. After a time the sense of presence of the lost limb becomes blunted, and it may in some cases entirely disappear. This may take place a few months after the amputation or the sensations may remain for years. Examples have been reported by Müller, in which the sense was undiminished thirteen, and in one case, twenty years after amputation. In a certain number of cases, however, the sense of the intermediate part is lost, the feeling in the hand or foot, as the case may be, remaining as distinct as ever, the impression being that the limb is gradually becoming shorter. It was noted by Gueniot, that the sense of the limb becoming shorter exists in about half of the cases of amputation in which cicatrization goes on regularly; and in these cases, the patient finally experiences a feeling as though the hand or foot were in direct contact with the stump.

*Physiological Differences between Motor and Sensory Nerve-Fibres.*—It has not been shown that there is any essential anatomical difference between the conducting elements of motor and sensory nerve-fibres; but the physiological differences are sufficiently distinct, as has already been seen. Under normal conditions, motor fibres conduct motor impulses in but one direction, and these fibres are insensible. Sensory fibres conduct impressions always in the opposite direction, and they do not conduct motor impulses. Certain experiments, however, have led some physiologists to adopt the view that the conducting properties of the nerves themselves, both motor and sensory, are identical, and that the direction of conduction depends upon the kind of centres with which nerves are connected. These experiments are the following:

It is said that the peripheral end of a divided motor nerve, the sublingual, can be made to unite with the central end of a sensory nerve, the lingual branch of the fifth; and that after a time motor impulses are conducted by the sensory fibres and sensory impressions, by the motor fibres. A careful study of these experiments, however, shows that the results are far from satisfactory.

Another experiment is grafting the end of the tail of a rat into the skin of the back (Bert). When the union has become complete, the tail is divided at its root and the sensory conduction, after five or six months, takes place in a direction opposite to the normal. While this experiment may be regarded as showing that sensory fibres may be made to assume such relations with other sensory fibres as to change, after a time, the direction of conduction, it has no absolutely direct bearing upon the question of the physiological identity of motor or sensory fibres.

The experiments just mentioned seldom succeed, and the results of union of motor with sensory nerves are quite indefinite; but the divided ends of mixed nerves readily reunite, and it is not difficult to establish a union between the central and peripheral ends of two different mixed nerves. It is hardly reasonable to assume that in these instances, each and every divided end of a motor fibre selects another motor fibre with which it unites, and that the same occurs with sensory fibres; but it would seem that in a divided mixed nerve, a certain number of fibres of each kind must unite with certain fibres that have similar physiological properties. Complete physiological regeneration of divided nerves is always slow, and frequently the regeneration never becomes complete. The fact, also, that curare destroys the physiological properties of motor nerves, leaving the sensory nerves intact, has a very important bearing upon the question under consideration; and anæsthetics temporarily abolish the physiological properties of the sensory nerves without necessarily affecting the motor nerves.

Until the results of experiments upon the artificial union of motor and sensory nerves become much more positive than they now are, it must be assumed that these two kinds of nerve-fibres have distinct physiological properties, both as regards the kind of impulse or impression produced by excitation or stimulation and the direction of conduction. It is possible, however, that these properties may be modified by altered relations for a long time with the trophic centres that influence the nutrition of the different kinds of nerve-fibres.

*Nervous Excitability.*—Immediately or soon after death, when the excitability of the nerves is at its maximum, they may be stimulated by mechanical, chemical or galvanic irritation, all of these agents producing contraction of the muscles to which the motor filaments are distributed. Mechanical irritation, simply pinching a portion of the nerve, for example, produces a single muscular contraction; but if the injury to the nerve be such as to disorganize its fibres, that portion of the nerve will no longer conduct an impulse. Among the irritants of this kind, are extremes of heat and cold. If an exposed nerve be cauterized, a vigorous muscular contraction follows. The same effect, though less marked, may be produced by the sudden application of intense cold. Among chemical reagents, there are some which excite the nerves and others which produce no effect; but these are not important from a physiological point of view, except common salt, which is sometimes used when it is desired to produce tetanic action. Mechanical stimulation and the action of certain chemicals are capable of exciting the nerves; but when their action goes so far as to disorganize the fibres, the conducting power of these fibres is lost. While, however, irritation of the nerve above the point of such injury has no effect, stimulation between this point and the muscles is still followed by contraction.

The most convenient method of exciting the nerves in physiological experiments is by means of electricity. This may be employed without disorganizing the nerve-tissue, and it consequently admits of extended and repeated application. The action of electricity, however, with the methods of preparing the nerves and muscles for experimentation, will be considered under a separate head.

*Rapidity of Nervous Conduction.*—The first accurate estimates of the rapidity of nervous conduction were made by Helmholtz, in 1850, and were applied to the motor nerves of the frog. These estimates were arrived at by an application of the graphic method, which was afterward considerably extended and improved by Marey. The process employed by Marey, which is essentially the same as that used in all recent investigations, is the following:

To mark small fractions of a second, a tuning-fork vibrating at a known rate (five hundred times in a second) is so arranged that a point connected with one of its arms is made to play against a strip of blackened paper. As the paper remains stationary, the point makes but a single mark; but when the paper moves, as the point vibrates a line is produced with regular curves, each curve representing $\frac{1}{500}$ of a second. If a lever be attached to a muscle and be so arranged as to indicate upon the paper, moving at the same rate, the instant when contraction takes place, it is evident that the interval between two contractions produced by stimulating the nerve at different points in its course may be accurately measured; and if the length of the nerve between the two points of stimulation be known, the difference in time will represent the rate of nervous conduction. In experiments upon frogs, the leg is prepared by cutting away the muscles and bone of the thigh, leaving the nerve attached. The lever is then applied to the muscles of the leg, and the nerve is stimulated successively at two points, the distance between them being measured.

Employing the myograph of Marey, Baxt, in the laboratory of Helmholtz, succeeded in measuring the rate of nervous conduction in the human subject. In these experiments, the swelling of the muscle during contraction was limited by enclosing the arm in a plaster-mould, and the contraction was observed through a small opening. By then exciting the contraction by stimulating the radial nerve successively at different distances from the muscle, the estimate was made. The rate in the human subject was thus estimated at one hundred and eleven feet (33·9 metres) per second.

The method used in determining the rate of conduction in motor nerves —an estimation of the difference in time of the passage of a stimulus applied to a nerve at two points situated at a known distance from each other—has been applied to the conduction of sensations. Hirsch made the first attempt to solve this question, in 1861. He employed the delicate chronometric instruments used in astronomy and noted the difference in time between the appreciation of an impression made upon a part of the body far removed from the brain, as the toe, and an impression made upon the cheek. This process admitted of a rough estimate of about one hundred and eleven feet (33·9 metres) per second as the rate of sensory conduction.

It is not necessary to describe fully the complicated apparatus by means of which the most recent estimates of the rate of nervous conduction have been made. The general results of the observations of Helmholtz, Marey, Baxt, Schleske and of many others nearly correspond with the estimates just given, and they show that the rate is about the same for motor and sensory nerves. This rate is modified by various conditions. It is diminished in the anelectrotonic and increased in the catelectrotonic condition of nerves. In the frog Helmholtz observed that the rate was very much reduced by cold, at 32° Fahr. (0° C.) being not more than one-tenth as rapid as at 60° or 70° Fahr. (15·5° or 21·11° C.).

The rate of transmission of impulses and impressions through the spinal cord has been investigated by calculating the distances between nerves as they are given off at different points and measuring the time required for the appreciation of certain impressions and the beginning of certain movements (Burkhardt). While these observations are not absolutely exact, their general results are of considerable physiological interest. According to Burkhardt, the rate of motor conduction in the cord is about one-third of the normal rate in the motor nerves. As compared with the sensory nerves, the cord conducts tactile impressions a little faster and painful impressions less than one half as fast.

Attempts have been made to estimate the duration of acts involving the central nervous system, such as the reflex phenomena of the spinal cord or the operations of the cerebral hemispheres. These have been partially successful, or, at least, they have shown that the reflex and the cerebral acts require a distinctly appreciable period of time. This in itself is an important fact; although the duration of these acts has not been measured with absolute accuracy. As the general result of experiments upon these points, it has been found that the reflex action of the spinal cord occupies more than twelve times the period required for the transmission of stimulus or impressions through the nerves. Donders found, in experiments upon his own person, that an act of volition required $\frac{1}{28}$ of a second, and one of simple distinction or recognition of an impression, $\frac{1}{25}$ of a second. These estimates, however, are merely approximate, and until they attain greater certainty, it is unnecessary to describe in detail the apparatus employed.

*Personal Equation.*—In recording astronomical observations, it has been found that a certain time elapsed between the actual observation of a phenomenon and the moment of its record. This error, which is equal to the interval of time between the impression made upon the retina and the muscular act by which a record is made, is not the same in different persons or even in the same person at all times. It may amount to $\frac{1}{5}$ of a second or even more, and it may be as low as $\frac{1}{50}$ of a second. If this difference be due to different rates of nervous conduction, and not entirely to variations in the rapidity of mental operations, it is evident that the velocity of the nerve-current must vary very considerably in different individuals.

*Action of Electricity upon the Nerves.*—So long as the nerves retain their excitability and anatomical integrity, they will respond to properly regulated electric stimulus. Experiments may be made upon the exposed nerves in living animals or in animals just killed; and of all classes, the cold-blooded animals present the most favorable conditions, on account of the persistence of nervous and muscular excitability for a considerable time after death. Experimenters most commonly use frogs, on account of the long persistence of the physiological properties of their tissues and the facility with which certain parts of the nervous system can be exposed. For ordinary experiments upon nervous conduction, the parts are prepared by detaching the posterior extremities, removing the skin, and cutting away the bone and muscles of the thigh, so as to leave the leg with the sciatic nerve attached. A frog's leg thus isolated presents a nervous trunk one or two inches (25 or 50 mm.) in length, attached to the muscles, which will respond to a feeble electric stimulus. It is by experiments made upon frogs prepared in this way that most of the important facts with regard to the action of electricity upon the nervous system have been developed.

In physiological experiments it is sometimes necessary to use different forms of electrical apparatus in order to study different properties and phenomena of nerve and muscle. A full description of the apparatus thus used would be out of place in this work, and it will be necessary only to enumerate and describe the different currents used and the manner of their application. Many of the phenomena, also, described by electro-physiologists, although curious and interesting, have little apparent application to human physiology or to the practice of medicine. A description of such phenomena may well be very brief in a work for the use of students and practitioners of medicine.

In studying the action of nerve and muscle, observers often use what is called a single Faradic, or induction shock. The duration of this stimulus is about $\frac{1}{1000}$ (0·0008) of a second (Helmholtz). The excitation, therefore, is practically instantaneous. These single shocks are produced by Du Bois-Reymond's apparatus, which is a modification of the Faradic, or induction battery. It will be seen farther on that somewhat different effects are produced by the stimulus due to closing and opening the circuit, and that with a feeble current, no contractions occur at any other time. The contractions thus produced are known respectively as opening and closing contractions. By the use of Du Bois-Reymond's keys, either the closing or the opening excitation may be diverted from the nerve, and a single closing or opening shock may be applied at will.

What is commonly known as an interrupted current is a Faradic, or induced current, in which the closing and opening excitations follow each other with greater or less rapidity, and the intervals may be regulated so that they occur at a regular rate. A rapid succession of induction-shocks produces a more or less prolonged muscular action, called tetanic contraction. The number of successive shocks in a second, required to produce a tetanic condition of a muscle, varies in different animals and in different muscles in the same animal. The minimum seems to be about sixteen per second, with a very considerable range of variation. Very rapid stimuli, even more than 24,000 per second, will produce tetanic contraction.

The Faradic, or induced current is different in its effects, under certain conditions of the nerves and muscles, from an interrupted galvanic, or primary current. This question is important in practical medicine, in determining the so-called "reaction of degeneration" of nerve and muscle.

The constant current, under certain conditions, has no effect that is indicated by muscular phenomena, contraction occurring only on closing or opening the circuit. This is known as the galvanic, or primary current. It produces, however, a peculiar condition of nerves and muscles, which will be described under the head of electrotonus. The primary current is derived directly from the cells of a galvanic battery, and this is to be distinguished from the Faradic, or induced current. The Faradic current is induced in a coil of small, insulated wire brought near and parallel to and partly or entirely surrounding a coil of larger wire carrying the primary current. When the circuit of the primary current is closed, the direction of the induced current is the reverse of that of the primary current. When the primary circuit is opened, the induced current has the same direction as the primary current. The direction of the primary current is uniform, but the direction of the induced current alternates with every interruption of the primary current. These induced currents are of momentary duration, being produced only when the primary current is closed and opened. A rapid interruption of the primary current is produced by what is called a rheotome, or current-interrupter, which is attached to all induction-batteries.

The points or surfaces used in closing a circuit in which a portion of nerve or muscle is included are called electrodes. They are usually designated as the copper, or positive electrode or pole, and the zinc, or negative electrode or pole. The positive pole is also called the anode, and the negative pole, the cathode. The direction of the current, when the circuit is closed, is from the anode to the cathode.

When a galvanic current is passed through a liquid or a moist, animal tissue, decomposition occurs, by what is known as electrolysis or internal polarization. The results of this decomposition, called ions, are of course different in different liquids or moist tissues. These accumulate at the poles and after a time disturb the currents and the phenomena produced. In animal tissues, acids accumulate at the anode, and alkalies, at the cathode. The ions which go to the anode are called anions, and those which accumulate at the cathode are called cations. In physiological experiments, it is often desirable to eliminate electrolysis, or internal polarization, and this is done by using the non-polarizable electrodes devised by Du Bois-Reymond. These may be described as follows: "The researches of Regnault, Matteucci and Du Bois-Reymond have proved that such electrodes can be made by taking two pieces of carefully amalgamated pure zinc wire, and dipping these in a saturated solution of zinc sulphate contained in tubes, their lower ends being closed by means of modeller's clay, moistened with a 0·6 per cent. normal saline solution. The contact of the tissues with these electrodes does not give rise to polarity." (Landois and Stirling.)

It is evident that the galvanic current may be applied to a nerve so that the direction may in the one case follow the course of the nerve, that is, from the centre to the periphery, and in the other, be opposite to the course of the nerve. These have been called respectively descending and ascending currents. When the positive pole (copper) is placed nearer the origin of the nerve, and the negative pole (zinc), below this point in the course of the nerve, the galvanic current follows the normal direction of the motor conduction, and this is called the descending current. When the poles are reversed and the direction is from the periphery toward the centre, it is called the ascending current. It will be convenient to speak of these two currents respectively as descending and ascending, in detailing experiments upon the action of electricity upon the nerves.

The points to be noted with regard to the effects of the application of electricity to an exposed nerve are the action of constant currents, the phenomena observed on closing and opening the circuit, and the effects of an interrupted current.

During the passage of a feeble constant current through a nerve, whatever be its direction, there are no convulsive movements and no evidences of pain. This fact has long been recognized by physiologists, who at first limited the effects of electricity upon the nerves to two periods, one at the closing of the circuit and the other at its opening. It will be seen, however, that the passage of electricity through a portion of a nervous trunk produces a peculiar condition in the nerve, which has been described under the name of electrotonus; but the fact remains that neither motion nor sensation is excited in a mixed nerve during the actual passage of a feeble constant current.

*Law of Contraction.*—All who have experimented upon the action of galvanism upon the nerves have noted the fact alluded to above, that contraction occurs only on closing or on opening the circuit. Take, for example, a frog's leg prepared with the nerve attached: Place one pole of a galvanic apparatus on the nerve and then make the connection, including a portion of the nerve in the circuit. With the feeblest current, contraction occurs only on closing the circuit. With what is called the "weak" current (Pflüger), contraction occurs only on closing the circuit, for currents in either direction. With the "moderate" current, contraction occurs both on closing and on opening the circuit, for currents in either direction. With the "strong" current, contraction occurs only on closing the circuit, with the descending current, and only on opening the circuit, with the ascending current. The above phenomena constitute what is called Pflüger's "law of contraction." The explanations of this law are the following:

The stimulus which gives rise to the closing contraction occurs at the cathode, when the electrotonus produced by the passage of the current begins. The stimulus which produces the opening contraction occurs at the anode, when the electrotonus disappears. The impulse is always stronger when the electrotonus begins than when it disappears. Therefore, when the current is so feeble that but one contraction is produced, this contraction occurs only on closing the circuit, for both ascending and descending currents.

With the "moderate" current, the strength of the opening impulse is sufficient to produce a contraction; and contractions therefore occur both on opening and closing the circuit, for both ascending and descending currents.

Strong currents produce closing contraction with the descending current, for the reason that the current destroys the conducting power of that portion of the nerve included between the poles of the battery, and, the stimulus occurring only at the cathode (see above), and the cathode being applied to that portion of the nerve nearest the muscle, the closing impulse only is conveyed to the muscle. The opening impulse (at the anode) is cut off from the muscle by the loss of conducting power in the intrapolar portion of the nerve. With the ascending current, the opening impulse, occurring at the anode, which is nearest the muscle, produces an opening contraction, and the closing impulse, which is at the cathode, is not conducted to the muscle.

While the constant current does not usually excite contractions during the time of its passage through a nerve, with a certain strength of current, the muscle is thrown into a tetanic condition. This is called "closing tetanus." When a constant current, not of sufficient strength to produce closing tetanus, is passed for several minutes through a long extent of nerve, a very vigorous contraction occurs on opening the circuit, which is followed by tetanus lasting for several seconds. This is called "opening tetanus." After a time, this varying with the excitability of the nerve and the strength of the current, the descending current will destroy the nervous excitability, but it may be restored by repose, or more quickly by the passage of an ascending current. If the ascending current be passed first for a few seconds, a contraction follows the opening of the circuit; and this contraction, within certain limits, is more vigorous the longer the current is passed. At the same time, the prolonged passage of the ascending current increases the excitability of the nerve for any kind of stimulus.

After a certain time, which varies in different animals, the nervous excitability becomes somewhat enfeebled by exposure of the parts. The phenomena then observed belong to the conditions involved in the process of "dying" of the nerve. In the later stages of this condition, the phenomena may be formulated as follows:

If the sciatic nerve attached to the leg of a frog, prepared in the usual way for such experiments, be subjected to a feeble galvanic current, there is a time when muscular contraction takes place only at the instant when the circuit is closed, no contraction occurring when the circuit is opened; and this occurs only with the descending current. With the ascending current, contraction of the muscles occurs only when the circuit is opened and none takes place when the circuit is closed. These phenomena are distinct after the excitability of the parts has become somewhat diminished by exposure or by electric stimulation of the nerve.

If a sufficiently powerful constant current be passed through a nerve, disorganization of its tissue takes place, and the nerve finally loses its excitability, as it does when bruised, ligatured, or when its structure is destroyed in any other way. It was thought by Galvani, and the idea has been adopted by Matteucci, Guérard and Longet, that a current directed exactly across a nerve, so as to pass at right angles to its fibres, does not give rise to muscular contraction. This view is generally accepted by physiologists.

The muscular contraction produced by electric stimulation of a nerve is more vigorous the greater the extent of the nerve included between the poles of the battery. This fact has long been observed, and its accuracy may easily be verified. It would naturally be expected that the greater the amount of stimulation, the more marked would be the muscular action; and the stimulation seems to be increased in proportion to the extent of nerve through which the current is made to pass.

The excitability of a nerve, it is well known, may be exhausted by the repeated application of electricity, whatever be the direction of the current, and it is more or less completely restored by repose. When it has been exhausted for the descending current, it will respond to the ascending current, and *vice versâ;* and after it has been exhausted by the descending current, it is restored more promptly by stimulation with the ascending current than by absolute repose, and *vice versâ*. This phenomenon, observed by Volta, is known as "voltaic alternation."

Many of the phenomena illustrating the law of contraction may be observed without the use of complicated apparatus. A form of battery, very convenient for some of these experiments, is the one described by Bernard. It consists simply of alternate copper and zinc wires wound around a piece of wood bent in the form of a horseshoe and terminating in two platinum points representing the positive and negative poles. This forms a sort of electric forceps, about eight inches (20 centimetres) long, which, when moistened with water slightly acidulated with acetic acid, will give a constant current of about the required strength.


FIG. 187.—*Electric forceps* (Liégeois). C, copper; Z, zinc.

The law of contraction is applicable to inhibitory nerves, as the inhibitory nerve of the heart, the difference being that the stimulation produces inhibition instead of contraction. It also holds good for sensory nerves, the effects being observed by noting the reflex contractions produced (Pflüger).

FIG. 188.—*Arrangement of frog's legs prepared so as to show induced contraction* (Liégeois).

A peculiar phenomenon, discovered by Matteucci, has been called "induced muscular contraction." If the nerve of a galvanoscopic frog's leg be placed in contact with the muscles of another leg prepared in the same way, stimulation of the nerve, giving rise to contraction of the muscles with which the nerve of the first leg is in contact, will induce contraction in the muscles of both. This experiment may be extended, and contractions may thus be induced in a series of legs, the nerve of one being in contact with the muscles of another. It is shown that "induced contraction" is not due to an actual propagation of the electric current but to a stimulus attending the muscular contraction itself, by the fact that the same phenomena occur when the first muscular contraction is produced by mechanical or chemical excitation of the nerve.

*Galvanic Current from the Exterior to the Cut Surface of a Nerve.*—Before studying certain phenomena presented in nerves of which a portion is subjected to the action of a constant galvanic current, it is important to note the fact that there exists in the nerves, as in the muscles, a galvanic current with a direction from the exterior to the cut surface. It has been roughly estimated that the nerve-current has one-eighth to one-tenth the intensity of the muscular current (Matteucci). The existence of the nerve-current has, as far as is known, no more physiological significance than the analogous fact observed in the muscular tissue. Galvanic currents also exist in the skin and in mucous membranes, the direction being from the outer surface, which is positive, to the inner surface, which is negative.

*Electrotonus, Anelectrotonus and Catelectrotonus.*—When a constant galvanic current is passed through a portion of a freshly prepared nerve, a large part of the entire nerve is brought into a peculiar electric condition (Du Bois-Reymond). While in this state, the nerve will deflect the needle of a galvanometer, and its excitability is modified. The deflection of the needle in this instance is not due to the normal nerve-current, for it occurs when the galvanometer is applied to the surface of the nerve only. It is due to an electric tension of the entire nerve, induced by the passage of a current through a portion of its extent. This condition is called electrotonus. There is also a peculiar condition of that portion of the nerve near the anode, differing from the condition of the nerve near the cathode. Near the anode the excitability of the nerve is diminished, and this condition is called ane-electrotonus. Near the cathode the excitability is increased, and this condition is called catelectrotonus (Pflüger). These phenomena have been the subject of extended investigation by electro-physiologists; and although the conditions are not to be included in the physiological properties of the nerves, they have considerable pathological and therapeutical importance. It is well known, for example, that electricity is often one of the most efficient agents at command for the restoration of the properties of nerves affected with disease; and the constant current has been extensively and successfully used as a therapeutical agent. The constant current, in restoring the normal condition of nerves, must influence, not only that portion included between the poles of the battery, but the entire nerve; and the electrotonic condition, with its modifications, in a measure explains how this result may be obtained.

The electrotonic condition is marked in proportion to the excitability of the nerve, and it is either entirely absent or extremely feeble in nerves that are dead or have lost their excitability. If a strong ligature be applied to the extrapolar portion of a nerve, or if the nerve be divided and the cut ends be brought in contact with each other, the electrotonic condition is either not observed or is very feeble. These facts show that the phenomena of electrotonus depend upon the physiological integrity of nerves. A dead nerve or one that has been divided or ligated may present these phenomena under the stimulation of a very powerful current—and then only to a slight degree—when the condition depends upon the purely physical properties of the nerve as a conductor; but these phenomena are not to be compared with those observed in nerves that retain their physiological properties.

As stated above, the electrotonic condition is not restricted to that portion of the nerve included between the poles of the battery. The condition of the portion between the poles is called intrapolar electrotonus, and the condition of the nerve outside of the poles is called extrapolar electrotonus.

When a portion of a nerve is subjected to a moderately strong constant current, the conditions of the extrapolar portions corresponding to the two poles of the battery are entirely different. Near the anode the excitability of the nerve and the rate of nervous conduction are diminished. If, however, a galvanometer be applied to this portion of the nerve, its electromotive power, measured by the deflection of the galvanometric needle, is increased. On the other hand, near the cathode the excitability of the nerve is increased, as well as the rate of nervous conduction, but the electromotive power is diminished.

The anelectrotonic condition, on the one hand, and the catelectrotonic condition, at the other pole of the battery, are marked in extrapolar portions of the nerve and are to be recognized, as well, in that portion through which the current is passing; but between the the poles, there is a point where these conditions meet, as it were, and where the excitability is unchanged. This has been called the neutral point. When the galvanic current is of moderate strength, the neutral point is about half-way between the poles. "When a weak current is used, the neutral point approaches the positive pole, while in a strong current, it approaches the negative pole. In other words, in a weak current the negative pole rules over a wider territory than the positive pole, whereas in a strong current the positive pole prevails" (Rutherford).

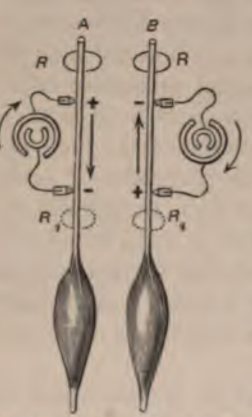



Fig. 189.—*Method of testing the excitability in electrotonus* (Landois).

The positive poles are + and the negative poles are —; R, $R_1$, R, $R_1$, points excited by the saline solution.

The conditions of extrapolar excitability vary with the direction of the current applied to the nerve. A convenient stimulus with which to measure this excitability is a solution of common salt, which excites more or less powerful tetanic contractions of the muscles. These variations are illustrated in Fig. 189.

In Fig. 189, A, a descending constant current is applied to the nerve. When the circuit is open, the salt applied to the nerve at R produces contractions of the muscle. If the circuit be closed, the contractions either become much less vigorous or cease, on account of the diminished excitability near the anode. This is called descending extrapolar anelectrotonus. If the salt be applied at $R_1$, the contractions are increased in vigor by closing the circuit, on account of the increased excitability of the nerve near the cathode. This is called ascending extrapolar catelectronus.

In Fig. 189, B, the conditions are reversed. The polarizing current here must be very weak, as a strong current may destroy the conducting power of the intrapolar portion of the nerve and thus prevent the conduction of the stimulus to the muscle when the salt is applied at R. On closing the circuit, there is ascending extrapolar catelectronus at R, and ascending extrapolar anelectronus at $R_1$.

Within certain limits, the greater the strength of the constant current applied to the nerve and the greater the length of nerve included between the poles of the battery, the greater is the deflection of the galvanoscopic needle, by which the electrotonic condition is measured.

Electrotonic conditions in sensory nerves are measured by reflex movements produced by the action of a stimulus applied to these nerves. The variations in excitability of inhibitory nerves, produced by a constant current, are indicated by increase or diminution in the inhibitory action. The phenomena in sensory and inhibitory nerves are analogous to those observed in motor nerves. The influence of a constant current upon the muscle current is distinct though feeble, producing a kind of electrotonic condition of muscle.

*Negative Variation.*—When a rapidly interrupted current is applied to a nerve so as to produce a tetanic condition of the muscles to which it is distributed, the normal or tranquil nerve-current is overcome, and a galvanoscopic needle applied to the nerve, which was first deviated by the nerve-current, will be observed to retrograde and will finally return to zero (Du Bois-Reymond). This may also be observed to a slight degree under the influence of mechanical or chemical stimulation of the nerve, the proper nerve-current being diminished, but generally not abolished. The variation of the needle under the influence of the tetanic condition has been called negative variation. It is not known that this has any important physiological or pathological significance.

# CHAPTER XVII.

## *SPINAL AND CRANIAL NERVES.*

Spinal nerves—Cranial nerves—Anatomical classification—Physiological classification—Motor oculi communis (third nerve)—Physiological anatomy—Properties and uses—Influence upon the movements of the iris—Patheticus, or trochlearis (fourth nerve)—Physiological anatomy—Properties and uses—Motor oculi externus, or abducens (sixth nerve)—Physiological anatomy—Properties and uses—Nerve of mastication (the small, or motor root of the fifth)—Physiological anatomy—Properties and uses—Facial, or nerve of expression (seventh nerve)—Physiological Anatomy—Intermediary nerve of Wrisberg—Alternate paralysis—General properties—Uses of the chorda tympani—Influence of various branches of the facial upon the movements of the palate and uvula—Spinal accessory (eleventh nerve)—Physiological anatomy—Uses of the internal branch from the spinal accessory to the pneumogastric—Influence of the spinal accessory upon the heart—Uses of the external, or muscular branch of the spinal accessory—Sublingual, or hypoglossal (twelfth nerve)—Physiological anatomy—Properties and uses—Trifacial, or trigeminal (fifth nerve)—Physiological anatomy—Properties and uses—Pneumogastric (tenth nerve)—Physiological anatomy—Properties and uses—General properties of the roots—Properties and uses of the auricular nerves—Properties and uses of the pharyngeal nerves—Properties and uses of the superior laryngeal nerves—Properties and uses of the inferior, or recurrent laryngeal nerves—Properties and uses of the cardiac nerves—Depressor-nerve of the circulation—Properties and uses of the pulmonary nerves—Properties and uses of the œsophageal nerves—Properties and uses of the abdominal nerves.

WITH a knowledge of the general properties of the nerves belonging to the cerebro-spinal system, it is easy to understand the uses of most of the special nerves, simply from their anatomical relations. This is especially true of the spinal nerves. These, in general terms, are distributed to the muscles of the trunk and extremities, to the sphincters and the integument covering these parts, the posterior segment of the head, and to certain mucous membranes. It is evident, therefore, that an account of the exact office of each nervous branch would necessitate a full description, not only of the nerves, but of the muscles of the body, which is manifestly within the scope only of treatises on descriptive anatomy.

### SPINAL NERVES.

There are thirty-one pairs of spinal nerves; eight cervical, twelve dorsal, five lumbar, five sacral and one coccygeal. Each nerve arises from the spinal cord by an anterior (motor) and a posterior (sensory) root, the posterior roots being the larger and each having a ganglion. Immediately beyond the ganglion, the two roots unite into a single mixed nerve, which passes out of the spinal canal by the intervertebral foramen. The nerve thus constituted is possessed of motor and sensory properties. It divides outside of the spinal canal into two branches, anterior and posterior, both containing motor and sensory filaments, which are distributed respectively to the anterior and the posterior parts of the body. The anterior branches are the larger, and they supply the limbs and all parts in front of the spinal column.

The anterior branches of the upper four cervical nerves form the cervical plexus, and the four inferior cervical nerves, with the first dorsal, form the brachial plexus. The anterior branches of the dorsal nerves, with the exception of the first, supply the walls of the chest and abdomen. These nerves go directly to their distribution and do not first form a plexus. The anterior branches of the upper four lumbar nerves form the lumbar plexus. The anterior branch of the fifth lumbar nerve and a branch from the fourth unite with the anterior branch of the first sacral, forming the lumbo-sacral nerve, and enter into the sacral plexus. The upper three anterior sacral nerves, with a branch from the fourth, form the sacral plexus. The greatest portion of the fourth anterior sacral is distributed to the pelvic viscera and the muscles of the anus. The fifth anterior sacral and the coccygeal are distributed to parts about the coccyx.

The posterior branches of the spinal nerves are very simple in their distribution. With one or two exceptions, which have no great physiological importance, these nerves pass backward from the main trunk, divide into two branches, external and internal, and their filaments of distribution go to the muscles and to integument behind the spinal column.

FIG. 190.—*Cervical portion of the spinal cord* (Hirschfeld).

FIG. 191.—*Dorsal portion of the spinal cord* (Hirschfeld).

FIG. 192.—*Inferior portion of the spinal cord, and cauda equina* (Hirschfeld).

1, antero-inferior wall of the fourth ventricle; 2, superior peduncle of the cerebellum; 3, middle peduncle of the cerebellum; 4, inferior peduncle of the cerebellum; 5, inferior portion of the posterior median columns of the cord; 6, glosso-pharyngeal nerve; 7, pneumogastric; 8, spinal accessory nerve; 9, 9, 9, 9, dentated ligament; 10, 10, 10, 10, *posterior roots of the spinal nerves*; 11, 11, 11, 11, *posterior lateral groove*; 12, 12, 12, 12, *ganglia of the posterior roots of the nerves*; 13, 13, *anterior roots of the nerves*; 14, *division of the nerves into two branches*; 15, lower extremity of the cord; 16, 16, coccygeal ligament; 17, 17, cauda equina; I-VIII, *cervical nerves*; I, II, III, IV-XII, *dorsal nerves*; I, II-V, *lumbar nerves*; I-V, *sacral nerves*.

It is farther important to note, that all of the cerebro-spinal nerves anastomose with the sympathetic.

## CRANIAL NERVES.

Many of the cranial nerves are peculiar, either as regards their general properties or in their distribution to parts concerned in special functions. In some of these nerves, the most important facts concerning their distribution have been ascertained only by physiological experimentation, and their anatomy is inseparably connected with their physiology. It would be desirable, if it were possible, to classify these nerves with reference strictly to their properties and uses; but this can be done only to a certain extent. The classification of the cranial nerves adopted by most anatomists is the arrangement of Sömmerring, in which the nerves are numbered from before backward, in the order in which they pass out of the skull, making twelve pairs.

### CLASSIFICATION OF THE CRANIAL NERVES.

*Nerves of Special Sense.*

Olfactory. (First pair.)
Optic. (Second pair.)
Auditory. (Eighth pair.)
Gustatory, comprising a part of the glosso-pharyngeal (ninth pair) and a small filament from the facial (seventh pair) to the lingual branch of the fifth pair.

*Nerves of Motion.*

Nerves of motion of the eyeball, comprising the motor oculi communis (third pair), the patheticus (fourth pair), and the motor oculi externus (sixth pair).

Nerve of mastication, or motor root of the fifth pair.

Facial, sometimes called the nerve of expression. (Seventh pair.)

FIG. 193.—*Roots of the cranial nerves* (Hirschfeld).
I. Olfactory.
II. Optic.
III. Motor oculi communis.
IV. Patheticus.
V. Nerve of mastication and trifacial.
VI. Motor oculi externus.
VII. Facial.
VIII. Auditory.
IX. Glosso-pharyngeal.
X. Pneumogastric.
XI. Spinal accessory.
XII. Sublingual.
The numbers 1 to 15 refer to branches which will be described hereafter.

Spinal accessory. (Eleventh pair.)
Sublingual. (Twelfth pair).

*Nerves of General Sensibility.*

Trifacial, or large root of the fifth pair.
A portion of the glosso-pharyngeal. (Ninth pair.)
Pneumogastric. (Tenth pair.)

In the above arrangement, the nerves are classified according to their properties at their roots. In their course, some of these nerves become mixed and their branches are both motor and sensory, such as the pneumogastric and the inferior maxillary branch of the trifacial.

The nerves of special sense have little or no general sensibility; and with the exception of the gustatory nerves, they do not present a ganglion on their roots, in this, also, differing from the ordinary sensory nerves. They are capable of conveying to the nerve-centres only certain peculiar impressions, such as odors, for the olfactory nerves, light, for the optic nerves, and sound, for the auditory nerves. The proper transmission of these impressions, however, involves the action of accessory parts, more or less complex; and the properties of these nerves will be fully considered in connection with the physiology of the special senses.

## Motor Oculi Communis (Third Nerve).

The third cranial nerve is the most important of the motor nerves distributed to the muscles of the eyeball. Its physiology is readily understood in connection with its distribution, the only point at all obscure being its relations to the movements of the iris, upon which the results of experiments are somewhat contradictory.

*Physiological Anatomy.*—The apparent origin of the third nerve is from the inner edge of the crus cerebri, directly in front of the pons Varolii, midway between the pons and the corpora albicantia. It presents here eight or ten filaments, of nearly equal size, which soon unite into a single, rounded trunk.

The deep origin of the nerve has been studied by dissections of the encephalon fresh and hardened by different liquids. From the groove by which they emerge from the encephalon, the fibres spread out in a fan-shape, the middle filaments passing inward, the anterior, inward and forward, and the posterior, inward and backward. It is probable that the middle filaments pass to the median line and decussate with corresponding fibres from the opposite side. The anterior filaments pass forward and are lost in the optic thalamus. The posterior filaments on either side pass backward to a gray nucleus beneath the aqueduct of Sylvius and here decussate with fibres from the opposite side. This decussation of the fibres of origin of the third nerves is important in connection with the harmony of action of the iris and the muscles of the eyes upon the two sides.

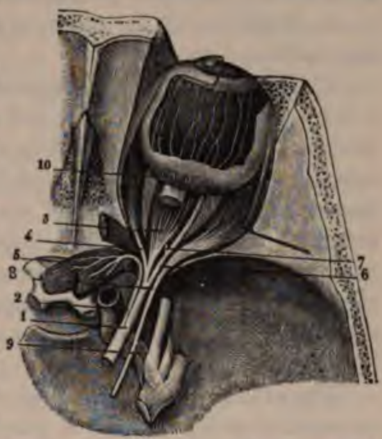



Fig. 194.—*Distribution of the motor oculi communis* (Hirschfeld).

1, *trunk of the motor oculi communis*; 2, *superior branch*; 3, *filaments which this branch sends to the superior rectus and the levator palpebri superioris*; 4, *branch to the internal rectus*; 5, *branch to the inferior rectus*; 6, *branch to the inferior oblique muscle*; 7, *branch to the lenticular ganglion*; 8, motor oculi externus; 9, filaments of the motor oculi externus anastomosing with the sympathetic; 10, *ciliary nerves.*

The distribution of the third nerve is very simple. As it passes into the orbit, by the sphenoidal fissure, it divides into two branches. The superior, which is the smaller, passes to the superior rectus muscle of the eye, and certain of its filaments are continued to the levator palpebræ superioris. The inferior division breaks up into three branches. The internal branch passes to the internal rectus muscle; the inferior branch, to the inferior rectus; the external branch, the largest of the three, is distributed to the inferior oblique muscle, and in its course, it sends a short and thick filament to the lenticular, or ophthalmic ganglion of the sympathetic. It is this branch which is supposed, through the short ciliary nerves passing from the lenticular ganglion, to furnish the motor influence to the iris. In its course this nerve receives a few very delicate filaments from the cavernous plexus of the sympathetic and a branch from the ophthalmic division of the trifacial.

*Properties and Uses of the Motor Oculi Communis.*—Stimulation of the root of the third nerve in a living animal produces contraction of the muscles to which it is distributed, but no pain. If the stimulus, however, be applied a little farther on in the course of the nerve, there are evidences of sensibility; and this is readily explained by its communications with the ophthalmic branch of the trifacial. At its root, therefore, this nerve is exclusively motor, and its office is connected entirely with the action of muscles.

The phenomena which are observed after section of the motor oculi communis in living animals are the following:

1. Falling of the upper eyelid, or blepharoptosis.

2. External strabismus, immobility of the eye except in an outward direction, inability to rotate the eye on its antero-posterior axis in certain directions, with slight protrusion of the eyeball.

3. Dilatation of the pupil, with a certain degree of interference with the movements of the iris.

The falling of the upper eyelid is constantly observed after division of the third nerve in living animals and always follows its complete paralysis in the human subject. An animal in which the nerve has been divided can not raise the lid, but can press the lids together by a voluntary effort. In the human subject the falling of the lid gives to the face a peculiar and characteristic expression. The complete loss of power shows that the levator palpebræ superioris muscle depends upon the third nerve entirely for its motor filaments. In pathology, external strabismus is frequently observed without falling of the lid, the filaments distributed to the levator muscle not being affected.

The external strabismus and the immobility of the eyeball except in an outward direction are due to paralysis of the internal, superior, and inferior recti muscles, the external rectus acting without its antagonist. This condition requires no farther explanation. These points are illustrated by the experiment of dividing the nerve in rabbits. If the head of the animal be turned inward, exposing the eye to a bright light, the globe will turn outward, by the action of the external rectus; but if the head be turned outward, the globe remains motionless.

It is somewhat difficult to note the effects of paralysis of the inferior oblique muscle, which also is supplied by the third nerve. This muscle, acting from its origin at the inferior and internal part of the circumference of the base of the orbit, to its attachment at the inferior and external part of the posterior hemisphere of the eyeball, gives to the globe a movement of rotation on an oblique, horizontal axis, downward and backward, directing the pupil upward and outward. When this muscle is paralyzed, the superior oblique, having no antagonist, rotates the globe upward and inward, directing the pupil downward and outward. The action of the oblique muscles is observed when the head is moved alternately toward one shoulder and the other. In the human subject, when the inferior oblique muscle on one side is paralyzed, the eye can not move in a direction opposite to the movements of the head, as it does upon the sound side, so as to keep the pupil fixed, and the patient has double vision.

When all the muscles of the eyeball, except the external rectus and superior oblique, are paralyzed, as they are by section of the third nerve, the globe is slightly protruded, simply by the relaxation of most of its muscles. An opposite action is easily observed in a cat with the facial nerve divided so that it can not close the lids. When the cornea is touched, all of the muscles, particularly the four recti, act to draw the globe into the orbit, which allows the lid to fall slightly, and projects the little membrane which serves as a third eyelid in these animals.

The third nerve sends a filament to the ophthalmic ganglion of the sympathetic, and from this ganglion, the short ciliary nerves take their origin and pass to the iris. While it is undoubtedly true that division of the third nerve affects the movements of the iris, it becomes a question whether this be a direct influence or an influence exerted primarily upon the ganglion, not perhaps, differing from the general effects upon the sympathetic ganglia that follow destruction of their branches of communication with the motor nerves.

Herbert Mayo (1823) made experiments on thirty pigeons, living or just killed, upon the action of the optic, the third and the fifth nerves, on the iris. When the third nerves were divided in the cranial cavity in a living pigeon, the pupils became fully dilated and did not contract on the admission of intense light; and when the same nerves were pinched in the living or dead bird, the pupils were contracted for an instant on each stimulation of the nerves. The same results followed division or stimulation of the optic nerves, under similar conditions; but when the third nerves had been divided, no change in the pupil ensued upon stimulating the entire or divided optic nerves.

The third nerves animate the muscular fibres that contract the pupil, the contraction produced by stimulation of the optic nerves being reflex in its character. Longet divided the motor oculi and the optic nerve upon the right side. He found that stimulation of the central end of the divided optic nerve produced no movement of the pupil of the side upon which the motor oculi had been divided, but caused contraction of the iris upon the opposite side. This, taken in connection with the fact that in amaurosis affecting one eye, the iris upon the affected side will not contract under the stimulus of light applied to the same eye, but will act when the uninjured eye is exposed to the light, farther illustrates the reflex action which takes place through these nerves.

The reflex action by which the iris is contracted is not instantaneous, like most of the analogous phenomena observed in the cerebro-spinal system, and its operations are rather characteristic of the action of the sympathetic system and the non-striated muscular tissue. It has been found, also, by Bernard, in experiments upon rabbits, that the pupil is not immediately dilated after division of the third nerve. The method employed by Bernard, introducing a hook into the middle temporal fossa through the orbit and tearing the nerve, can hardly be accomplished without touching the ophthalmic branch of the fifth, which produces intense pain and is always followed by a more or less persistent contraction of the pupil. Several hours after the operation, however, the pupil is generally found dilated, and it may slowly contract when the eye is exposed to the light. In one experiment this occurred after the eye had been exposed for an hour. Farther experiments have shown that although the pupil contracts feebly and slowly under the stimulus of light after division of the motor oculi, it will dilate under the influence of belladonna and can be made to contract by operating upon other nerves. It is well known, for example, that division or stimulation of the fifth nerve produces contraction of the pupil. This takes place after as well as before division of the third nerve. Section of the sympathetic in the cervical region also contracts the pupil, and this occurs after paralysis of the motor oculi. These facts show that the third nerve is not the only one capable of acting upon the iris and that it is not the sole avenue for the transmission of reflex influences.

Bernard also found that stimulation of the motor oculi itself did not produce contraction of the pupil, but this result followed when he stimulated the ciliary nerves coming from the ophthalmic ganglion. Chauveau, in experiments upon horses, did not observe contraction of the pupil following stimulation of the motor oculi, although it was sometimes seen in rabbits. At all events, contraction is by no means constant; and when it occurs, it probably depends upon stimulation of the ciliary nerves themselves or irritation of the ophthalmic branch of the fifth, and not upon stimulation of the trunks of the third pair. When the eye is turned inward by a voluntary effort, the pupil is contracted; and when the axes of the two eyes are made to converge strongly, as in looking at near objects, the contraction is very considerable (Müller).

The third nerve contains filaments which preside over voluntary movements of the ciliary muscle in the accommodation of the eye to vision at different distances.

The following case illustrates, in the human subject, nearly all of the phenomena following paralysis of the motor oculi communis, in experiments upon the lower animals:

The patient was a girl, nineteen years of age, with complete paralysis of the nerve upon the left side. There was slight protrusion of the eyeball, complete ptosis, with the pupil moderately dilated and insensible to ordinary impressions of light. The sight was not affected, but there was double vision, except when objects were placed before the eyes so that the axes were parallel, or when an object was seen with but one eye. The axis of the left eye was turned outward, but it was not possible to detect any deviation upward or downward. Upon causing the patient to incline the head alternately to one shoulder and the other, it was evident that the affected eye did not rotate in the orbit but moved with the head. This seemed to be a case of complete and uncomplicated paralysis of the third nerve.

### PATHETICUS, OR TROCHLEARIS (FOURTH NERVE).

The physiology of the patheticus is very simple and resolves itself into the action of a single muscle, the superior oblique.

*Physiological Anatomy.*—The apparent origin of the patheticus is from the superior peduncles of the cerebellum; but it may be easily followed to the valve of Vieussens. The deep roots can be traced, passing from without inward, to the following parts: One filament is lost in the substance of the peduncles; other filaments pass from before backward into the valve of Vieussens and are lost, and a few pass into the frenulum; a few filaments pass backward and are lost in the corpora quadrigemina; but the greatest number pass to the median line and decussate with corresponding filaments from the opposite side. The fibres can be traced to a nucleus in the floor of the aqueduct of Sylvius, beneath the nucleus of the third nerve. The decussation of the fibres of origin of the fourth nerve has the same physiological significance as the decussation of the roots of the third. From this origin, the patheticus passes into the orbit, by the sphenoidal fissure, and is distributed to the superior oblique muscle of the eyeball. In the cavernous sinus it receives branches of communication from the ophthalmic branch of the fifth, but these are not closely united with the nerve. A small branch passes into the tentorium, and one joins the lachrymal nerve, these, however, being exclusively sensory and coming from the ophthalmic branch of the fifth. It also receives a few filaments from the sympathetic.


FIG. 195.—*Distribution of the patheticus* (Hirschfeld).

1, olfactory nerve; II, optic nerves; III, motor oculi communis; IV, *patheticus, by the side of the ophthalmic branch of the fifth, and passing to the superior oblique muscle*; VI, motor oculi externus; 1, ganglion of Gasser; 2, 3, 4, 5, 6, 7, 8, 9, 10, ophthalmic division of the fifth nerve, with its branches.

*Properties and Uses of the Patheticus.*—Direct observations upon the patheticus in living animals have shown that it is motor, and its stimulation excites contraction of the superior oblique muscle only. This muscle arises just above the inner margin of the optic foramen, passes forward, along the upper wall of the orbit at its inner angle, to a little, cartilaginous ring which serves as a pulley. From its origin to this point it is muscular. Its tendon becomes rounded just before it passes through the pulley, where it makes a sharp curve, passes outward and slightly backward, and becomes spread out to be attached to the globe, at the superior and external part of its posterior hemisphere. It acts upon the eyeball from the pulley at the upper and inner portion of the orbit as the fixed point and rotates the eye upon an oblique, horizontal axis, from below upward, from without inward and from behind forward. By its action, the pupil is directed downward and outward. It is the antagonist of the inferior oblique, the action of which has been described in connection with the motor oculi communis. When the patheticus is paralyzed, the eyeball is immovable, as far as rotation is concerned. When the head is moved toward the shoulder, the eye does not rotate to maintain the globe in the same relative position, and there is double vision.

### Motor Oculi Externus, or Abducens (Sixth Nerve).

Like the patheticus, the motor oculi externus is distributed to but a single muscle. Its uses, therefore, are apparent from a study of its distribution and properties.

*Physiological Anatomy.*—The apparent origin of the sixth nerve is from the groove separating the anterior corpus pyramidale of the medulla oblongata from the pons Varolii, from the upper portion of the medulla and from the lower portion of the pons, next the groove. Its origin at this point is by two roots: an inferior, which is the larger and comes from the corpus pyramidale; and a superior root, sometimes wanting, which seems to come from the lower portion of the pons. All anatomists are agreed that the deep fibres of origin of this nerve pass to the gray matter in the floor of the fourth ventricle. Vulpian followed these fibres to within about two-fifths of an inch (10 mm.) of the median line, but they could not be traced beyond this point. It is not known that the fibres of the two sides decussate. From this origin the nerve passes into the orbit by the sphenoidal fissure and is distributed exclusively to the external rectus muscle of the eyeball. In the cavernous sinus it anastomoses with the sympathetic through the carotid plexus and receives a filament from Meckel's ganglion. It also receives sensory filaments from the ophthalmic branch of the fifth. It is thought by some anatomists that this nerve occasionally sends a small filament to the ophthalmic ganglion; and it was stated by Longet that this branch, which is exceptional, exists in those cases in which paralysis of the motor oculi communis, which usually furnishes all the motor filaments to this ganglion, is not attended with immobility of the iris.

Fig. 196.—*Distribution of the motor oculi externus* (Hirschfeld).

1, trunk of the motor oculi communis, with its branches (2, 3, 4, 5, 6, 7); 8, *motor oculi externus, passing to the external rectus muscle*; 9, *filaments of the motor oculi externus, anastomosing with the sympathetic*; 10, ciliary nerves.

*Properties and Uses of the Motor Oculi Externus.*—Direct experiments have shown that the motor oculi externus is entirely insensible at its origin, its stimulation producing contraction of the external rectus muscle and no pain. The same experiments illustrate the action of the nerve, inasmuch as its stimulation is followed by contraction of the muscle and deviation of the eye outward. Division of the nerve in the lower animals or its paralysis in the human subject is attended with internal, or converging strabismus, due to the unopposed action of the internal rectus muscle.

With regard to the associated movements of the eyeball, it is important to note that all of the muscles of the eye which have a tendency to direct the pupil inward or to produce the simple movements upward and downward (the internal, inferior, and superior recti) are animated by a single nerve, the motor oculi communis, this nerve also supplying the inferior oblique; and that each of the two muscles that move the globe so as to direct the pupil outward, except the inferior oblique (the superior oblique and the external rectus), is supplied by a special nerve. The movements of the eyeball will be described more minutely in connection with the physiology of vision.

### Nerve of Mastication (the Small, or Motor Root of the Fifth Nerve).

The motor root of the fifth nerve is entirely distinct from its sensory portion, until it emerges from the cranial cavity, by the foramen ovale. It is then closely united with the inferior maxillary branch of the large root; but at its origin it has been shown to be motor, and its section in the cranial cavity has demonstrated its distribution to a particular set of muscles.

*Physiological Anatomy.*—The apparent origin of the fifth nerve is from the lateral portion of the pons Varolii. The small, or motor root arises from a point a little higher and nearer the median line than the large root, from which it is separated by a few fibres of the white substance of the pons. At the point of apparent origin, the small root presents six to eight rounded filaments. If a thin layer of the pons covering these filaments be removed, the roots will be found penetrating its substance, becoming flattened, passing under the superior peduncles of the cerebellum and going to a gray nucleus, with large multipolar cells, in the anterior wall of the fourth ventricle, near the median line. At this point, the fibres change their direction, passing from without inward and from behind forward toward the median line, the fibres diverging rapidly. The posterior fibres pass to the median line, and certain of them decussate with fibres from the opposite side. The anterior fibres pass toward the aqueduct of Sylvius and are lost. The fibres become changed in their character when they are followed inward beyond the anterior wall of the fourth ventricle. Here they lose their white color, become gray and present a number of globules of gray substance between their filaments.

From the origin above described, the small root passes beneath the ganglion of Gasser—from which it sometimes, though not constantly, receives a filament of communication—lies behind the inferior maxillary branch of the large root, and passes out of the cranial cavity, by the foramen ovale. Within the cranium the two roots are distinct; but after the small root passes through the foramen, it is united by a mutual interlacement of fibres with the sensory branch.

The inferior maxillary nerve, made up of the motor root and the inferior maxillary branch of the sensory root, just after it passes out by the foramen ovale, divides into two branches, anterior and posterior. The anterior branch, which is the smaller, is composed almost entirely of motor filaments and is distributed to the muscles of mastication. It gives off five branches. The first of these passes to be distributed to the masseter muscle, in its course occasionally giving off a small branch to the temporal muscle and a filament to the articulation of the inferior maxilla with the temporal bone. The two deep temporal branches are distributed to the temporal muscle. The buccal branch sends filaments to the external pterygoid and the temporal muscles, and a small branch is distributed to the internal pterygoid muscle. From the posterior branch, which is chiefly sensory but contains some motor filaments, branches are sent to the mylo-hyoid muscle and to the anterior belly of the digastric. In addition the motor branch of the fifth sends filaments to the tensor muscles of the velum palati.


FIG. 197.—*Distribution of the small root of the fifth nerve* (Hirschfeld).

1, *branch to the masseter muscle*; 2, *filament of this branch to the temporal muscle*; 3, *buccal branch*; 4, *branches anastomosing with the facial nerve*; 5, *filament from the buccal branch to the temporal muscle*; 6, *branches to the external pterygoid muscle*; 7, *middle deep temporal branch*; 8, auriculo-temporal nerve; 9, temporal branches; 10, auricular branches; 11, anastomosis with the facial nerve; 12, lingual branch; 13, *branch of the small root to the mylo-hyoid muscle*; 14, inferior dental nerve, with its branches (15, 15); 16, mental branch; 17, anastomosis of this branch with the facial nerve.

The above description gives in general terms the distribution of the nerve of mastication, without taking into consideration its various anastomoses, the most important of which are with the facial. Experiments have shown that the buccinator muscle receives no motor filaments from the fifth but is supplied entirely by the facial. The buccal branch of the fifth sends motor filaments only, to the external pterygoid and the temporal, its final branches of distribution being sensory and going to integument and to mucous membrane.

In treating of the physiology of digestion, a table has been given of the muscles of mastication, with a description of their action. It will be seen by reference to this table that the following muscles depress the lower jaw; viz., the anterior belly of the digastric, the mylo-hyoid, the genio-hyoid and the platysma myoides. Of these the digastric and the mylo-hyoid are animated by the motor root of the fifth; the genio-hyoid is supplied by filaments from the sublingual; and the platysma myoides, by branches from the facial and from the cervical plexus. All of the muscles which elevate the lower jaw and move it laterally and antero-posteriorly; viz., the temporal, masseter, and the internal and external pterygoids—the muscles most actively concerned in mastication—are animated by the motor root of the fifth.

*Properties and Uses of the Nerve of Mastication.*—The anatomical distribution of the small root of the fifth nerve points at once to its uses. Charles Bell, whose ideas of the nerves were derived almost entirely from their anatomy, called it the nerve of mastication, in 1821, although he did not state that any experiments were made with regard to its action. All anatomical and physiological writers since that time have adopted this view. It would be difficult if not impossible to stimulate the root in the cranial cavity in a living animal; but its Faradization in animals just killed determines very marked movements of the lower jaw. Experiments have demonstrated the physiological properties of the small root, which is without doubt solely a nerve of motion.

The observations upon section of the fifth pair in the cranial cavity are most important in connection with the uses of its sensory branches and will be referred to in detail in treating of the properties of the large root. In addition to the loss of sensibility following section of the entire nerve, Bernard noted the effects of division of the small root, which can not be avoided in the operation. In rabbits the paralysis of the muscles of mastication upon one side, and the consequent action of the muscles upon the unaffected side only, produce, a few days after the operation, a remarkable change in the appearance of the incisor teeth. As the teeth in these animals are gradually worn away in mastication and reproduced, the lower jaw being deviated by the action of the muscles of the sound side, the upper incisor of one side and the lower incisor of the other touch each other but slightly and the teeth are worn unevenly. This makes the line of contact between the four incisors, when the jaws are closed, oblique instead of horizontal.

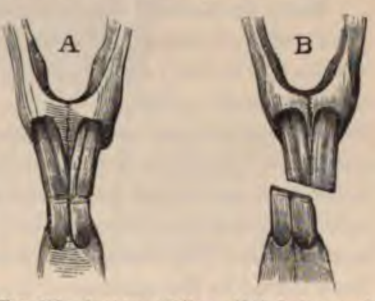


FIG. 198.—*Incisors of the rabbit, before and after section of the nerve of mastication* (Bernard).
A, incisors, normal condition.
B, incisors, seven days after section of the nerve on one side.

There is little left to say with regard to the uses of the motor root of the fifth nerve, in addition to the description of the action of the muscles of mastication, contained in the chapters on digestion, except as regards the action of the filaments sent to the muscles of the velum palati. In deglutition the muscles of mastication are indirectly involved. This act can not be well performed unless the mouth be closed by these muscles. When the food is brought in contact with the velum palati, muscles are brought into action which render this membrane tense, so that the opening is adapted to the size of the alimentary bolus. These muscles are animated by the motor root of the fifth. This nerve, then, is not only the nerve of mastication, animating all of the muscles concerned in this act, except two of the most unimportant depressors of the lower jaw (the genio-hyoid and the platysma myoides), but it is concerned indirectly in deglutition.

### Facial, or Nerve of Expression (Seventh Nerve).

The anatomical relations of the facial nerve are quite intricate and it communicates freely with other nerves. As far as can be determined by experiments upon living animals, this nerve is exclusively motor at its origin; but in its course it presents anastomoses with the sympathetic, with branches of the fifth and with the cervical nerves, undoubtedly receiving sensory filaments.

*Physiological Anatomy.*—The facial nerve has its apparent origin from the lateral portion of the medulla oblongata, in the groove between the olivary and restiform bodies, just below the border of the pons Varolii, its trunk being internal to the trunk of the auditory nerve. It is separated from the auditory by the two filaments constituting what is known as the intermediary nerve of Wrisberg, or the portio inter duram et mollem. As this little nerve joins the facial, it is usually included in its root.

Many anatomists have endeavored to trace the fibres of the facial from their point of emergence from the encephalon to their true origin, but with results not entirely satisfactory. Its fibres pass inward, with one or two deviations from a straight course, to the floor of the fourth ventricle, where they spread out and become fan-shaped. In the floor of the fourth ventricle certain of the fibres have been thought to terminate in the cells of the gray substance, and others have been traced to the median line, where they decussate; the course of most of the fibres, however, has not been satisfactorily established. The fibres of origin of the intermediary nerve of Wrisberg have been traced to the nucleus of the glosso-pharyngeal.

It is evident from physiological experiments, that the decussation of the fibres in the floor of the fourth ventricle itself is not very important. Vulpian made, in dogs and rabbits, a longitudinal section in the middle line of the ventricle, which would necessarily have divided the fibres passing from one side to the other, without producing notable paralysis of the facial nerves upon either side. This single fact is sufficient to show that the main decussation of the fibres animating the muscles of the face takes place, if at all, at some other point.

The pathological facts bearing upon the question of decussation of the filaments of origin of the facial have long been recognized. They are in brief as follows: When there is a lesion of the brain-substance anterior to the pons Varolii, the phenomena due to paralysis of the facial are observed upon the same side as the hemiplegia, opposite the side of injury to the brain. When the lesion is either in the pons or below it, the face is affected upon the same side, and not upon the side of the hemiplegia. This is called alternate paralysis. In view of these facts, the phenomenon of hemiplegia upon one side and facial paralysis upon the other is regarded as indicating, with tolerable certainty, that the injury to the brain has occurred upon the same side as the facial paralysis, either within or posterior to the pons Varolii.

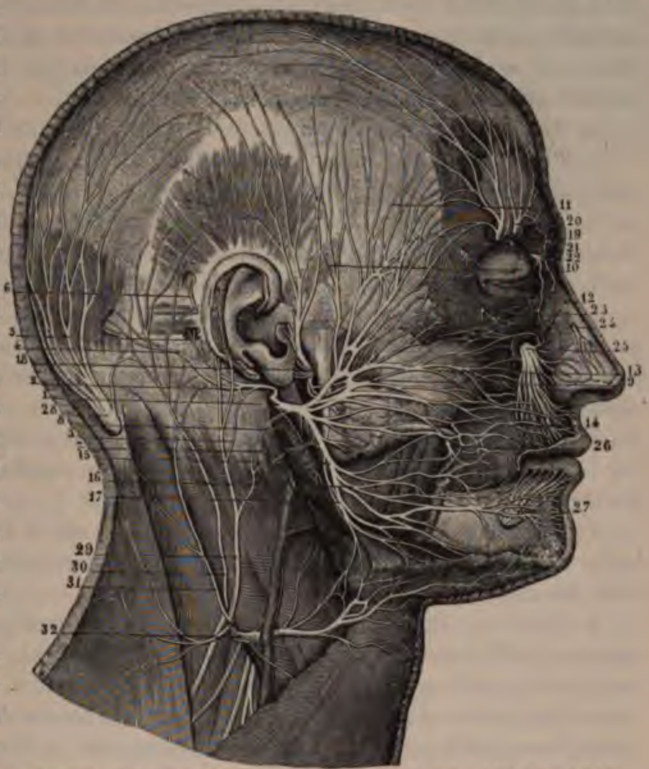


FIG. 199.—*Superficial branches of the facial and the fifth* (Hirschfeld). 1, *trunk of the facial*; 2, *posterior auricular nerve*; 3, *branch which it receives from the cervical plexus*; 4, *occipital branch*; 5, 6, *branches to the muscles of the ear*; 7, *digastric branches*; 8, *branch to the stylo-hyoid muscle*; 9, *superior terminal branch*; 10, *temporal branches*; 11, *frontal branches*; 12, *branches to the orbicularis palpebrarum*; 13, *nasal, or sub-orbital branches*; 14, *buccal branches*; 15, *inferior terminal branch*; 16, *mental branches*; 17, *cervical branches*; 18, superficial temporal nerve (branch of the fifth); 19, 20, frontal nerves (branches of the fifth); 21, 22, 23, 24, 25, 26, 27, branches of the fifth; 28, 29, 30, 31, 32, branches of the cervical nerves.

As already stated, the fibres of origin of the facial have been traced to the floor of the fourth ventricle, where a few decussate but most of them are lost. The question now is, whether or not the fibres pass up through the pons and decussate above, as the pathological facts just noted would seem to indicate. Anatomical researches upon this point are not satisfactory, and the existence of such a decussation has never been clearly demonstrated. The pathological observations, nevertheless, remain; and however indefinite anatomical researches may have been, there can be no doubt that lesions in one lateral half of the pons affect the facial upon the same side, while lesions above have a crossed action. The most that can be said upon this point is that it is a reasonable inference from pathological facts that the nerves decussate anterior to the pons.

The main root of the facial, the auditory nerve and the intermediary nerve of Wrisberg pass together into the internal auditory meatus. At the bottom of the meatus, the facial and the nerve of Wrisberg enter the aquæductus Fallopii, following its course through the petrous portion of the temporal bone. In the aqueduct the nerve of Wrisberg presents a little, gangliform enlargement (geniculate ganglion) of a reddish color, which has been shown to contain nerve-cells. The main root and the intermediary nerve then unite and form the common trunk of the facial, which emerges from the cranial cavity, by the stylo-mastoid foramen.

In the aquæductus Fallopii the facial gives off the following branches:

1. The large petrosal branch is given off at the ganglioform enlargement and goes to Meckel's ganglion.

2. The small petrosal branch is given off at the ganglioform enlargement or a very short distance beyond it and passes to the otic ganglion.

3. A small branch, the tympanic, is distributed to the stapedius muscle.

4. The chorda tympani passes through the cavity of the tympanum and joins the lingual branch of the inferior maxillary division of the fifth, as it passes between the two pterygoid muscles, with which nerve it becomes closely united.

5. Opposite to the point of origin of the chorda tympani, a communicating branch passes between the facial and the pneumogastric, connecting these nerves by a double inosculation.

The five branches above described are given off in the aquæductus Fallopii. The following branches are given off after the nerve has emerged from the cranial cavity:

1. Just after the facial has passed out at the stylo-mastoid foramen, it sends a small, communicating branch to the glosso-pharyngeal nerve. This branch is sometimes wanting.

2. The posterior auricular nerve is given off by the facial, a little below the stylo-mastoid foramen. Its superior branch is distributed to the retrahens aurem and the attollens aurem, In its course this nerve receives a communicating branch of considerable size from the cervical plexus, by the auricularis magnus. It sends some filaments to the integument. The inferior, or occipital branch, the larger of the two, is distributed to the occipital portion of the occipito-frontalis muscle and to the integument.

3. The digastric branch is given off near the root of the posterior auricular. It is distributed to the posterior belly of the digastric muscle. In its course it anastomoses with filaments from the glosso-pharyngeal nerve. From the plexus formed by this anastomosis, filaments are given off to the digastric and to the stylo-hyoid muscle.

4. Near the stylo-mastoid foramen, a small branch is given off, which is distributed exclusively to the stylo-hyoid muscle.

5. Near the stylo-mastoid foramen, or sometimes a little above it, a long, delicate branch is given off, which is not noticed in many works on anatomy. It is described, however, by Hirschfeld, under the name of the lingual branch. It passes behind the stylo-pharyngeal muscle, and then by the sides of the

pharynx to the base of the tongue. In its course it receives one or two branches from the glosso-pharyngeal nerve, which are nearly as large as the original branch from the facial. As it passes to the base of the tongue, it anastomoses again by a number of filaments with the glosso-pharyngeal. It then sends filaments of distribution to the mucous membrane and finally passes to the stylo-glossus and palato-glossus muscles.

Having given off these branches, the trunk of the facial passes through the parotid gland, dividing into its two great terminal branches:

1. The temporo-facial branch, the larger, passes upward and forward to be distributed to the superficial muscles of the upper part of the face; viz., the attrahens aurem, the frontal portion of the occipito-frontalis, the orbicularis palpebrarum, corrugator supercilii, pyramidalis nasi, levator labii superioris, levator labii superioris alæque nasi, the dilators and compressors of the nose, part of the buccinator, the levator anguli oris and the zygomatic muscles. In its course it receives branches of communication from the auriculo-temporal branch of the inferior maxillary nerve. It joins also with the temporal branch of the superior maxillary and with branches of the ophthalmic. It thus becomes a mixed nerve and is distributed in part to integument.

2. The cervico-facial nerve passes downward and forward to supply the buccinator, orbicularis oris, risorius, levator labii inferioris, depressor labii inferioris, depressor anguli oris and platysma.

*General Properties of the Facial Nerve.*—It has long been recognized that the facial is the motor nerve of the superficial muscles of the face and that its division produces paralysis of motion and no marked effects upon sensation. It is evident, also, from the communications of the facial with the fifth, that it probably contains in its course sensory fibres. Indeed, all who have operated upon this nerve have found that it is slightly sensory after it has emerged from the cranial cavity. It is a question, however, of great importance to determine whether or not the facial be endowed with sensibility by virtue of its own fibres of origin. The main root is evidently from the motor tract, resembles the anterior roots of the spinal nerves, and is distributed to muscles; but this root is joined by the intermediary nerve of Wrisberg, which presents a small, ganglionic enlargement, that is analogous to the ganglia upon the posterior roots of the spinal nerves. The testimony of direct experimentation is in favor of the insensibility of the facial at its origin. It is true that the intermediary nerve of Wrisberg has a certain anatomical resemblance to the sensory nerves, chiefly by reason of its ganglioform enlargement; but direct experiments are wanting to show that it is sensory.

*Uses of the Branches of the Facial given off within the Aqueduct of Fallopius.*—The first branch, the large petrosal, is the motor root of Meckel's ganglion. This will be referred to again, in connection with the sympathetic system. The second branch, the small petrosal, is one of the motor roots of the otic ganglion of the sympathetic. The third branch, the tympanic, is distributed exclusively to the stapedius muscle. The second and third branches will be again considered, in connection with the physiology of the internal ear. The fourth branch, the chorda tympani, is so important that it demands special consideration. The fifth branch is given off opposite the origin of the chorda tympani and passes to the pneumogastric, to which nerve it probably supplies motor filaments. In this branch, sensory filaments pass from the pneumogastric and constitute a part of the sensory connections of the facial.

*Uses of the Chorda Tympani.*—This nerve passes between the bones of the ear and through the tympanic cavity, to the lingual branch of the inferior maxillary division of the fifth, which it joins at an acute angle, between the pterygoid muscles. As regards the portion of the facial which furnishes the filaments of the chorda tympani, it is nearly certain that these come from the intermediary nerve of Wrisberg.

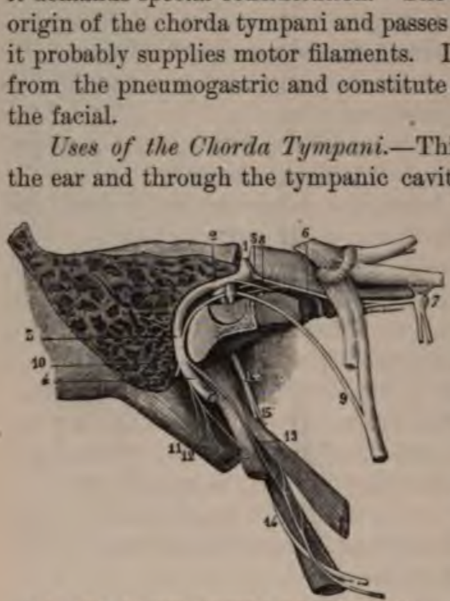


FIG. 200.—*Chorda-tympani nerve* (Hirschfeld).
1, 2, 3, 4, facial nerve passing through the aquæductus Fallopii; 5, ganglioform enlargement (geniculate ganglion); 6, great petrosal nerve; 7, spheno-palatine ganglion; 8, small petrosal nerve; 9, *chorda tympani*; 10, 11, 12, 13, various branches of the facial; 14, 14, 15, glosso-pharyngeal nerve.

There can be no doubt with regard to the influence of the chorda tympani upon the sense of taste in the anterior two-thirds of the tongue. In cases of disease or injury in which the root of the facial is involved so that the chorda tympani is paralyzed, in addition to the ordinary phenomena of paralysis of the superficial muscles of the face, there is loss of taste in the anterior two-thirds of the tongue, upon the side corresponding to the lesion. The action of the chorda tympani will be considered again, in connection with the physiology of gustation.

*Influence of Various Branches of the Facial upon the Movements of the Palate and Uvula.*—There can be little doubt that filaments from the facial animate certain of the movements of the velum palati and uvula. It has been observed that in certain cases of facial paralysis the palate upon one side is flaccid and the uvula is drawn to the opposite side; but these phenomena do not occur unless the nerve be affected at its root or within the aquæductus Fallopii. It is true that the uvula frequently is drawn to one side or the other in persons unaffected with facial paralysis, but it is none the less certain that it is deviated as a consequence of paralysis of the facial in some instances. The filaments of the facial which influence the levator palati and azygos uvulæ muscles are derived from the large petrosal branch of the nerve, passing to the muscles through Meckel's ganglion, the filaments to the palato-glossus and the palato-pharyngeus being given off from the glosso-pharyngeal, but originally coming from an anastomosing branch of the facial (Longet). As regards the branches of communication from the glosso-pharyngeal, Longet has mentioned a preparation by Richet, in the museum of the *École de médecine*, of Paris, in which branches of the facial upon one side pass directly to the palato-glossus and the palato-pharyngeus, without any connection with the glosso-pharyngeal nerve. In the anatomical description of the branches of the facial, it has already been noted that a filament, described by Hirschfeld, passes to the stylo-glossus and the palato-glossus muscles. This is the filament affected when there is deviation of the point of the tongue.

In view of the examples of paralysis of the palate and uvula in certain cases of facial palsy, the frequent occurrence of contractions of the muscles of these parts upon stimulation of the facial and the reflex action through the glosso-pharyngeal and the facial, there can be little doubt that the muscles of the palate and uvula are animated by filaments derived from the seventh nerve. The effects of paralysis of these muscles are manifested by more or less trouble in deglutition and in the pronunciation or certain words, with great difficulty in the expulsion of mucus collected in the back part of the mouth and the pharynx.

*Uses of the External Branches of the Facial.*—The general action of the branches of the facial going to the superficial muscles of the face is sufficiently evident, in view of what is known of the distribution of these branches and the general properties of the nerve. Throughout the writings of Charles Bell, the facial is spoken of as the "respiratory nerve of the face." It is now recognized as the nerve which presides over the movements of the superficial muscles of the face, not including those directly concerned in the act of mastication. This being its general action, it is easy to assign to each of the external branches of the facial its particular office.

Just after the facial nerve has passed out at the stylo-mastoid foramen, it sends to the glosso-pharyngeal the communicating branch, the action of which has just been mentioned in connection with the movements of the palate.

The posterior auricular branch, becoming partly sensory by the addition of filaments from the cervical plexus, gives sensibility to the integument on the back part of the ear and over the occipital portion of the occipito-frontalis muscle. It animates the retrahens and the attollens aurem, muscles that are little developed in man but are very important in certain of the inferior animals. It also animates the posterior portion of the occipito-frontalis muscle.

The branches distributed to the posterior belly of the digastric and to the stylo-hyoid muscle simply animate these muscles, one of the uses of which is to assist in deglutition. The same may be said of the filaments that go to the stylo-glossus.

The two great branches distributed upon the face, after the trunk of the nerve has passed through the parotid gland, have the most prominent action. Both of these branches are slightly sensory, from their connections with other nerves, and are distributed in small part to integument.

The temporo-facial branch animates all of the muscles of the upper part of the face. In complete paralysis of this branch, the eye is constantly open, even during sleep, on account of paralysis of the orbicularis muscle. In cases of long standing, the globe of the eye may become inflamed from constant exposure, from abolition of the movements of winking by which the tears are distributed over its surface and little foreign particles are removed, and, in short, from absence of the protective action of the lids. In these cases the lower lid may become slightly everted. The frontal portion of the occipito-frontalis, the attrahens aurem, and the corrugator supercilii muscles, are also paralyzed. The most prominent symptom of paralysis of these muscles is inability to corrugate the brow upon one side.

Paralysis of the muscles that dilate the nostrils has been shown to have an important influence upon respiration through the nose. It was the synchronism between the acts of dilatation of the nostrils and the movements of inspiration which first led Charles Bell to regard the facial as a respiratory nerve. In instances of complete paralysis of the nostril of one side, there is frequently some difficulty in inspiration, even in the human subject.

Charles Bell and others have also noted an interference with olfaction, due to the inability to inhale with one nostril, in cases of facial paralysis.

FIG. 201.

FIG. 202.

FIG. 203.

FIG. 204.

FIG. 205.

FIG. 206.

*Expressions of the face produced by contraction of the muscles under electrical excitation* (Le Bon, after Duchenne).

Fig. 201, front view of the face in repose.
Fig. 202, profile view.
Fig. 203, expression of laughter upon one side, produced by contraction of the zygomaticus major.
Fig. 204, expression of fear, produced by contraction of the frontal muscle and the depressors of the lower jaw.
Fig. 205, expression of fear, profile view.
Fig. 206, expression of fear and great pain, produced by contraction of the corrugator supercilii and the depressors of the lower jaw.

The influence of the nerve in the act of conveying odorous emanations to the olfactory membrane is sufficiently evident, after what has been said concerning the action of the facial in respiration.

The effects of paralysis of the other superficial muscles of the face are manifested in the distortion of the features, on account of the unopposed action of the muscles upon the sound side, a phenomenon which is sufficiently familiar. When facial palsy affects one side and is complete, the angle of the mouth is drawn to the opposite side, the eye upon the affected side is widely and permanently opened, even during sleep, and the face has upon that side a peculiarly expressionless appearance. When a patient affected in this way smiles or attempts to grimace, the distortion is much increased. The lips are paralyzed upon one side, which sometimes causes a flow of saliva from the corner of the mouth. In the lower animals that use the lips in prehension, paralysis of these parts interferes considerably with the taking of food. The flaccidity of the paralyzed lips and cheek in the human subject sometimes causes a puffing movement with each act of expiration, as if the patient were smoking a pipe.

The buccinator is not supplied by filaments from the nerve of mastication but is animated solely by the facial. Paralysis of this muscle interferes materially with mastication, from a tendency to accumulation of the food between the teeth and the cheek. Patients complain of this difficulty, and they sometimes keep the food between the teeth by pressure with the hand. In the rare instances in which both facial nerves are paralyzed, there is very great difficulty in mastication, from the cause just mentioned.

The action of the external branches of the facial is thus sufficiently simple; and it is only as its deep branches affect the sense of taste, the movements of deglutition, etc., that it is difficult to ascertain their exact office. As this is the nerve of expression of the face, it is in the human subject that the phenomena attending its paralysis are most prominent. When both sides are affected, the aspect is remarkable, the face being absolutely expressionless and looking as if it were covered with a mask.

### SPINAL ACCESSORY (ELEVENTH NERVE).

The spinal accessory nerve, from the great extent of its origin, its important anastomoses with other nerves and its peculiar course and distribution, has long engaged the attention of anatomists and physiologists, who have advanced many theories with regard to its office. Its physiological history, however, begins with comparatively recent experiments, which alone have given a positive knowledge of its properties and uses.

*Physiological Anatomy*—The origin of this nerve is very extensive. A certain portion arises from the lower half of the medulla oblongata, and the rest takes its origin below, from the upper two-thirds of the cervical portion of the spinal cord. That portion of the root which arises from the medulla oblongata is called the bulbar portion, the roots from the cord constituting the spinal portion. Inasmuch as there is a marked difference between the uses of these two portions, the anatomical distinction just mentioned is important.

The superior roots arise by four or five filaments, from the lower half of the medulla oblongata, below the origin of the pneumogastrics. These filaments of origin pass to a gray nucleus in the medulla, below the origin of the pneumogastric.

The spinal portion of the nerve arises from the upper part of the spinal cord, between the anterior and posterior roots of the upper four or five cervical nerves. The filaments of origin are six to eight in number. The most inferior of these is generally single, the other filaments frequently being arranged in pairs. These take their origin from the lateral portion of the cord and are connected with the anterior cornua of gray matter.

Following the nerve from its most inferior filament of origin upward, it gradually increases in size by union with its other roots, enters the cranial cavity by the foramen magnum, and passes to the jugular foramen, by which it emerges, with the glosso-pharyngeal, the pneumogastric and the internal jugular vein.

In its course the spinal accessory anastomoses with several nerves. Just as it enters the cranial cavity, it receives filaments of communication from the posterior roots of the upper two cervical nerves. These filaments, however, are not constant. It frequently though not constantly sends a few filaments to the superior ganglion, or the ganglion of the root of the pneumogastric. After it has emerged by the jugular foramen it sends a branch of considerable size to the pneumogastric, from which nerve it also receives a few filaments of communication. In its course it also receives filaments of communication from the anterior branches of the second, third, and fourth cervical nerves.

FIG. 207.—*Spinal accessory nerve* (Hirschfeld). 1, trunk of the facial nerve; 2, 2, glosso-pharyngeal nerve; 3, 3, pneumogastric; 4, 4, 4, *trunk of the spinal accessory*; 5, sublingual nerve; 6, superior cervical ganglion; 7, 7, anastomosis of the first two cervical nerves; 8, carotid branch of the sympathetic; 9, 10, 11, 12, 13, branches of the glosso-pharyngeal; 14, 15, branches of the facial; 16, otic ganglion; 17, auricular branch of the pneumogastric; 18, *anastomosing branch from the spinal accessory to the pneumogastric*; 19, anastomosis of the first pair of cervical nerves with the sublingual; 20, *anastomosis of the spinal accessory with the second pair of cervical nerves*; 21, *pharyngeal plexus*; 22, superior laryngeal nerve; 23, external laryngeal nerve; 24, middle cervical ganglion.

In its distribution the spinal accessory presents two branches. The internal, or anastomotic branch, passes to the pneumogastric just below the plexiform enlargement which is sometimes called the ganglion of the trunk of the pneumogastric. This branch is composed principally if not entirely of the filaments that take their origin from the medulla oblongata. As it joins the pneumogastric it subdivides into two smaller branches. The first of these forms a portion of the pharyngeal branch of the pneumogastric. The second becomes intimately united with the pneumogastric, lying at its posterior portion, and furnishes filaments to the inferior, or recurrent laryngeal branch, which is distributed to all of the muscles of the larynx except the crico-thyroid. The passage of the filaments from the spinal accessory to the pharyngeal branch of the pneumogastric is easily observed; but the fact that filaments from this nerve pass to the larynx by the recurrent laryngeal has been ascertained by physiological experiments.

The external, or large branch of the spinal accessory, called the muscular branch, penetrates and passes through the posterior portion of the upper third of the sterno-cleido-mastoid muscle, and goes to the anterior surface of the trapezius, which muscle receives its ultimate branches of distribution. In its passage through the sterno-cleido-mastoid, it joins with branches from the second and third cervical nerves and sends filaments of distribution to the muscle. Although the two muscles just mentioned receive motor filaments from the spinal accessory, they are also supplied from the cervical nerves; and consequently they are not entirely paralyzed when the spinal accessory is divided.

*Properties and Uses of the Spinal Accessory.*—Notwithstanding the great difficulty in exposing and operating upon the roots of the spinal accessory, it has been demonstrated that their stimulation produces convulsive movements in certain muscles. By stimulating the filaments that arise from the medulla oblongata, contractions of the muscles of the pharynx and larynx are produced, but no movements of the sterno-mastoid and trapezius. Stimulation of the roots arising from the spinal cord produces movements of the two muscles just mentioned and absolutely no movements in the larynx (Bernard). In view of these experiments, it is evident that the true filaments of origin of the spinal accessory are motor; and it is farther evident that the filaments from the medulla oblongata are distributed to the muscles of the pharynx and larynx, while the filaments from the spinal cord go to the sterno-cleido-mastoid and trapezius.

The trunk of the spinal accessory, after the nerve has passed out of the cranial cavity, has a certain degree of sensibility. If the nerve be divided, the peripheral extremity manifests recurrent sensibility, but the central end is also sensible, probably from direct filaments of communication from the cervical nerves and the pneumogastric.

*Uses of the Internal Branch from the Spinal Accessory to the Pneumogastric.*—Bischoff attempted to ascertain the uses of this branch by dividing the roots of the spinal accessory upon both sides in a living animal. The results of his experiments may be stated in a very few words: He attempted to divide all of the roots of the nerves upon both sides by dissecting down to the occipito-atloid space and penetrating into the cavity of the spinal canal. In the first three experiments upon dogs, the animals died so soon after section of the nerves, that no satisfactory results were obtained. In two succeeding experiments upon dogs, the animals recovered. After division of the nerves the voice became hoarse, but a few weeks later it became normal. On killing the animals, an examination of the parts showed that some of the filaments of origin had not been divided. An experiment was then made upon a goat, but this was unsatisfactory, as the roots were not completely divided. Finally another experiment was made upon a goat. In this the results were more satisfactory. After division of the nerve upon one side, the voice became hoarse. As the filaments were divided upon the opposite side, the voice was enfeebled, until finally it became extinct. The sound emitted afterward was one which could in nowise be called voice ("*qui neutiquam vox appellari potuit*"). This experiment was made in the presence of Tiedemann and Seubertus and was not repeated.

Bernard, who determined exactly the influence of the spinal accessory over the vocal movements of the larynx, first repeated the experiments of Bischoff; but the animals operated upon died so soon, from hæmorrhage or other causes, that his observations were not satisfactory. After many unsuccessful trials, he succeeded in overcoming all difficulties, by following the trunk of the nerve back to the jugular foramen, seizing it here with a strong forceps and drawing it out by the roots. The operation is generally most successful in cats, although Bernard succeeded frequently in other animals.

When one spinal accessory is extirpated, the vocal sounds are hoarse and unnatural. When both nerves are torn out, in addition to the disturbance of deglutition and the partial paralysis of the sterno-mastoid and trapezius muscles, the voice becomes extinct. Animals operated upon in this way move the jaws and make evident efforts to cry, but no vocal sound is emitted. Bernard kept animals, with both nerves extirpated, for several months and did not observe any return of the voice. His observations, which have been fully confirmed, show that the internal branch of the spinal accessory is the nerve of phonation. The filaments which preside over the vocal movements of the larynx pass in greatest part through the recurrent laryngeal branches of the pneumogastrics; but the recurrent laryngeals also contain motor filaments from other sources, which latter are concerned in the respiratory movements of the glottis.

*Influence of the Internal Branch of the Spinal Accessory upon Deglutition.*—There are two ways in which deglutition is affected through this nerve: 1. When the larynx is paralyzed as a consequence of extirpation of both nerves, the glottis can not be completely closed to prevent the entrance of foreign bodies into the air-passages. In rabbits particularly, it has been noted that particles of food penetrate the trachea and find their way into the lungs. 2. The spinal accessory furnishes filaments to the pharyngeal branch of the pneumogastric, and through this nerve, it directly affects the muscles of deglutition; but the muscles animated in this way by the spinal accessory have a tendency to draw the lips of the glottis together, while they assist in passing the alimentary bolus into the œsophagus. When these important acts are wanting, there is some difficulty in the process of deglutition itself, as well as danger of the passage of foreign particles into the larynx.

*Influence of the Spinal Accessory upon the Heart.*—The spinal accessory furnishes to the pneumogastric the inhibitory fibres which influence the action of the heart. A sufficiently powerful Faradic current, passed through one pneumogastric only, will in some animals arrest the cardiac movements. Waller found that if he extirpated the spinal accessory upon one side, after four or five days the action of the heart could not be arrested by stimulating the pneumogastric upon the same side; but inhibition followed stimulation of the pneumogastric upon the opposite side, on which the connections with the spinal accessory were intact. In these observations, it seemed necessary that a sufficient time should elapse after extirpation of the spinal accessory for the excitability of the filaments that join the pneumogastric to become extinct; but the experiments are sufficient to show the direct inhibitory influence of the spinal accessory upon the heart. After extirpation of the spinal accessory, degenerated fibres are found in the trunk of the pneumogastric. The mechanism of inhibition of the heart has already been considered in connection with the physiology of the circulation.

*Uses of the External, or Muscular Branch of the Spinal Accessory.*— Observations have shown that the internal branch of the spinal accessory, and the internal branch only, is directly concerned in the vocal movements of the larynx, and to a great extent, in the closure of the glottis during deglutition. It has been noted, in addition, that animals in which both branches have been extirpated present irregularity of the movements of the anterior extremities and suffer from shortness of breath after violent muscular exertion. The use of the corresponding extremities in the human subject is so different, that it is not easy to make a direct application of these experiments; still, certain inferences may be drawn from them with regard to the action of the external branch in man.

In prolonged vocal efforts, the vocal chords are put upon the stretch, and the act of expiration is different from that in tranquil breathing. In singing, for example, the shoulders frequently are fixed; and this is done to some extent by the action of the sterno-cleido-mastoid and the trapezius. It is probable, then, that the action of the branch of the spinal accessory which goes to these muscles has a certain synchronism with the action of the branch going to the larynx and the pharynx; the one fixing the upper part of the chest so that the expulsion of the air through the glottis may be more nicely regulated by the expiratory muscles, and the other acting upon the vocal chords.

In what is known as muscular effort, the glottis is closed, the thorax is fixed after a full inspiration, and respiration is arrested so long as the effort, if it be not too prolonged, is continued. The same synchronism, therefore, obtains in this as in prolonged vocal efforts. In experiments in which the muscular branch only has been divided, shortness of breath, after violent muscular effort, is observed; and this is probably due to the want of synchronous action of the sterno-cleido-mastoid and trapezius. The irregularity in the movements of progression in animals in which either both branches or the muscular branches alone have been divided is due to anatomical peculiarities. Bernard has observed these irregularities in the dog and the horse, but they are not so well marked in the cat. There have been no opportunities for illustrating these points in the human subject.

## SUBLINGUAL (TWELFTH NERVE).

The last of the motor cranial nerves is the sublingual; and its action is intimately connected with the physiology of the tongue in deglutition and articulation, although the sublingual is also distributed to certain of the muscles of the neck.

*Physiological Anatomy.*—The apparent origin of the sublingual is from the medulla oblongata, in the groove between the olivary body and the anterior pyramid, on the line of the anterior roots of the spinal nerves. At this point, its root is formed of ten to twelve filaments, which extend from the inferior portion of the olivary body to about the junction of the upper with the middle third of the medulla. These filaments of origin are separated into two groups, superior and inferior. From this apparent origin, the filaments have been traced into the gray matter of the floor of the fourth ventricle, between the deep origin of the pneumogastric and the glosso-pharyngeal. Although there is much difference of opinion upon this point, it is probable that some of the filaments of origin of these nerves decussate in the floor of the fourth ventricle. The superior and inferior filaments of origin of the nerve unite to form two bundles, which pass through distinct perforations in the dura mater. These two bundles then pass into the anterior condyloid foramen and unite into a single trunk as they emerge from the cranial cavity.

After the sublingual has passed out of the cranial cavity, it anastomoses with several nerves. It sends a filament of communication to the sympathetic as it branches from the superior cervical ganglion. Soon after it has passed through the foramen, it sends a branch to the pneumogastric. It anastomoses by two or three branches with the upper two cervical nerves, the filaments passing in both directions between the nerves. It anastomoses with the lingual branch of the fifth, by two or three filaments passing in both directions.

In its distribution the sublingual presents several peculiarities:

Its first branch, the descendens noni, passes down the neck to the sterno-hyoid, sterno-thyroid and omo-hyoid muscles.

The thyro-hyoid branch is distributed to the thyro-hyoid muscle.

The other branches are distributed to the stylo-glossus, hyo-glossus, genio-hyoid and genio-hyo-glossus muscles, their terminal filaments going to the intrinsic muscles of the tongue.

It is thus seen that the sublingual nerve is distributed to all of the muscles in the infra-hyoid region, the action of which is to depress the larynx and the hyoid bone after the passage of the alimentary bolus through the pharynx; to one of the muscles in the supra-hyoid region, the genio-hyoid; to most of the muscles which move the tongue; and to the muscular fibres of the tongue itself. The action of these muscles and of the tongue itself in deglutition has already been fully discussed.

*Properties and Uses of the Sublingual.*—The fact that the sublingual nerve arises from a continuation of the motor tract of the spinal cord and has no ganglion upon its main root would lead to the supposition that it is an exclusively motor nerve. In operating upon the roots of the spinal accessory—when the origin of the sublingual is necessarily exposed—Longet has irritated the roots in the dog, without any evidence of pain on the part of the animal. Such experiments, taken in connection with the anatomical characters of the nerve, render it almost certain that its root is devoid of

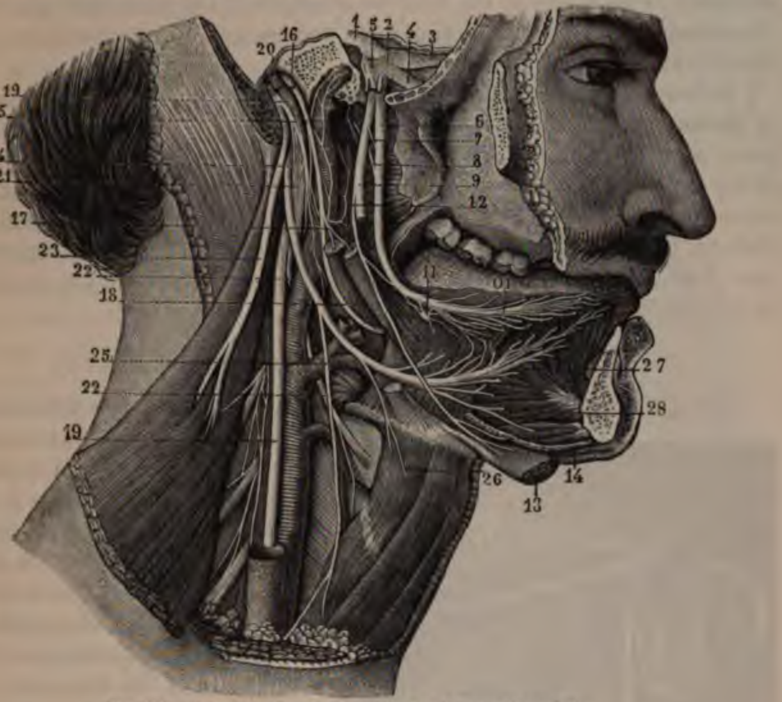



FIG. 208.—*Distribution of the sublingual nerves* (Sappey).

1, root of the fifth nerve; 2, ganglion of Gasser; 3, 4, 5, 6, 7, 9, 10, 12, branches and anastomoses of the fifth nerve; 11, submaxillary ganglion; 13, anterior belly of the digastric muscle; 14, section of the mylo-hyoid muscle; 15, glosso-pharyngeal nerve; 16, ganglion of Andersch; 17, 18, branches of the glosso-pharyngeal nerve; 19, 19, pneumogastric; 20, 21, ganglia of the pneumogastric; 22, 22, superior laryngeal branch of the pneumogastric; 23, spinal accessory nerve; 24, *sublingual nerve*; 25, *descendens noni*; 26, *thyro-hyoid branch*; 27, *terminal branches*; 28, *two branches, one to the genio-hyo-glossus and the other to the genio-hyoid muscle.*

sensibility at its origin. All modern experimenters have confirmed the observations of Mayo and of Magendie, with regard to the sensibility of the sublingual after it has passed out of the cranial cavity. The anastomoses of this nerve with the upper two cervical nerves, with the pneumogastric, and with the lingual branch of the fifth, afford a ready explanation of this fact.

The sublingual may be easily exposed in the dog by making an incision just below the border of the lower jaw, dissecting down to the carotid artery and following the vessel upward until the nerve is seen as it crosses its course. On applying a feeble Faradic current at this point, there are evidences of sensibility, and the tongue is moved at each stimulation.

The phenomena following section of both sublingual nerves point directly to their uses. The most notable fact observed after this operation is that the movements of the tongue are entirely lost, while general sensibility and the sense of taste are not affected. The phenomena which follow division of these nerves consist simply in loss of power over the tongue, with considerable difficulty in deglutition.

In the human subject the sublingual is usually more or less affected in hemiplegia. In these cases, as the patient protrudes the tongue the point is deviated. This is due to the unopposed action of the genio-hyo-glossus upon the sound side, which, as it protrudes the tongue, directs the point toward the side affected with paralysis.

A disease of rather rare occurrence has been described under the name of glosso-labial-paralysis, which is characterized by paralysis of the sublinguals, affecting also the orbicularis oris and frequently the intrinsic muscles of the larynx. The phenomena referable to the loss of power over the tongue correspond to those observed in animals after section of the sublingual nerves. Patients affected in this way experience difficulty in deglutition, and in addition there is some interference with articulation, which can not be observed in experiments upon animals.

### TRIFACIAL (LARGE ROOT OF THE FIFTH NERVE).

A single nerve, the large root of the fifth pair, called the trifacial or the trigeminal, gives general sensibility to the face and to the head as far back as the vertex. This nerve is important, not only as the great sensitive nerve of the face, but from its connections with other nerves and its relations to the organs of special sense.

FIG. 209.—*Principal branches of the large root of the fifth nerve* (Robin).

*a, ganglion of Gasser; a–w, ophthalmic division of the fifth; b, ophthalmic ganglion; c, branch from the ophthalmic division of the fifth to the ophthalmic ganglion; d,* motor oculi communis; *e,* carotid; *f,* ciliary nerves; *g,* cornea and iris; *a–h, superior maxillary division of the fifth; i, two branches from the superior maxillary division of the fifth to the spheno-palatine ganglion; j,* deep petrosal nerve; *k,* filaments from the motor root of the fifth to the internal muscle of the malleus; *l,* naso-palatine ganglion; *m,* otic ganglion; *n,* small superficial petrosal nerve; *o, branches of the fifth to the submaxillary ganglion; p, branches to the sublingual gland; q,* facial nerve; *r,* sympathetic ganglion; *s,* nerve of mastication; *t, chorda tympani, joining the lingual branch of the fifth; u,* Vidian nerve; *v,* branch from the motor root, to the internal pterygoid muscle; *w, branch of the fifth to the lachrymal gland; x,* bend of the facial nerve; *y,* middle meningeal artery; *z,* filament from the carotid plexus, to the ophthalmic ganglion; (1 and 2 are not in the figure) 3, external spheno-palatine filaments; 4, spheno-palatine ganglion; 5, naso-palatine nerve; 6, anterior palatine nerve; 7, *inferior maxillary division of the fifth;* 8, nerve of Jacobson.

*Physiological Anatomy.*—The apparent origin of the large root of the fifth is from the lateral portion of the pons Varolii, posterior and inferior to the origin of the small root, from which it is separated by a few transverse fibres of white substance. The deep origin is far removed from its point of emergence from the encephalon. The roots pass entirely through the substance of the pons, from without inward and from before backward, without any connection with the fibres of the pons itself. By this course the fibres reach the medulla oblongata, where the roots divide into three bundles. The anterior bundle passes from behind forward, between the anterior fibres of the pons and the cerebellar portion of the restiform bodies, to anastomose with the fibres of the auditory nerve. The other bundles, which are posterior, pass, the one in the anterior wall of the fourth ventricle to the lateral tract of the medulla oblongata, and the other, becoming grayish in color, to the restiform bodies, from which they may be followed as far as the point of the calamus scriptorius, A few fibres from the two sides decussate at the median line, in the anterior wall of the fourth ventricle. From this origin, the large root of the fifth passes obliquely upward and forward to the ganglion of Gasser, which is situated in a depression in the petrous portion of the temporal bone, on the internal portion of its anterior face.


FIG. 210.—*Ophthalmic division of the fifth* (Hirschfeld).
1, *ganglion of Gasser*; 2, *ophthalmic division of the fifth*; 3, *lachrymal branch*; 4, *frontal branch*; 5, *external frontal*; 6, *internal frontal*; 7, *supratrochlear*; 8, *nasal branch*; 9, *external nasal*; 10, *internal nasal*; 11, anterior deep temporal nerve; 12, middle deep temporal nerve; 13, posterior deep temporal nerve; 14, origin of the superficial temporal nerve; 15, great superficial petrous nerve.
I to XII, roots of the cranial nerves.

The Gasserian ganglion is semilunar in form, with its concavity looking upward and inward. At the ganglion the nerve receives filaments of communication from the carotid plexus of the sympathetic. This anatomical point is of importance in view of some of the remote effects which follow division of the fifth nerve through the ganglion in living animals.

At the ganglion of Gasser, from its anterior and external portion, are given off a few small and unimportant branches to the dura mater and the tentorium.

From the convex border of the ganglion the three great divisions, or branches arise, which have given to the nerve the name of trifacial or trigeminal. These are: 1, the ophthalmic; 2, the superior maxillary; 3, the inferior maxillary. The ophthalmic and superior maxillary branches are derived entirely from the sensory root. The inferior maxillary branch joins with the motor root and forms a mixed nerve.

The ophthalmic branch, the first division of the fifth, is the smallest of the three. Before it enters the orbit it receives filaments of communication from the sympathetic, sends small branches to all of the motor nerves of the eyeball and gives off a small recurrent branch which passes between the layers of the tentorium.

Just before the ophthalmic branch enters the orbit by the sphenoidal fissure it divides into three branches, the lachrymal, frontal and nasal.

The lachrymal, the smallest of the three, sends a branch to the orbital branch of the superior maxillary nerve, passes through the lachrymal gland, to which certain of its filaments are distributed, and its terminal filaments go to the conjunctiva and to the integument of the upper eyelid.

The frontal branch, the largest of the three, divides into the supratrochlear and supraörbital nerves. The supratroachlear passes out of the orbit between the supraörbital foramen and the pulley of the superior oblique muscle. It sends in its course a long, delicate filament to the nasal branch and is finally lost in the integument of the forehead. The supraörbital passes through the supraörbital foramen, sends a few filaments to the upper eyelid, and supplies the forehead, the anterior and the median portions of the scalp, the mucous membrane of the frontal sinus, and the pericranium covering the frontal and parietal bones.

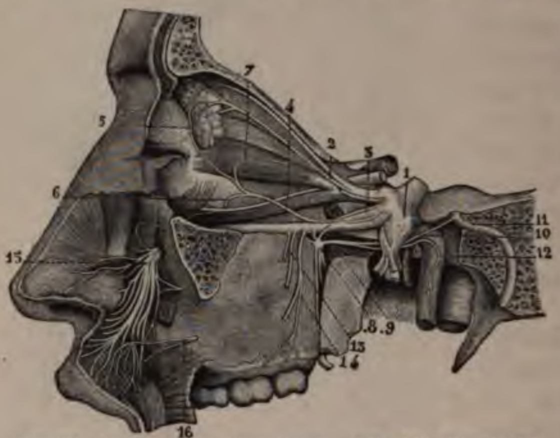


FIG. 211.—*Superior maxillary division of the fifth* (Hirschfeld). 1, ganglion of Gasser; 2, lachrymal branch of the ophthalmic division; 3, *superior maxillary division of the fifth*; 4, *orbital branch*; 5, *lachrymo-palpebral filament*; 6, *malar branch*; 7, *temporal branch*; 8, *spheno-palatine ganglion*; 9, Vidian nerve; 10, great superficial petrosal nerve; 11, facial nerve; 12, branch of the Vidian nerve; 13, *anterior and two posterior dental branches*; 14, *branch to the mucous membrane of the alveolar processes*; 15, *terminal branches of the superior maxillary division*; 16, branch of the facial.

The nasal branch, before it penetrates the orbit, gives off a long, delicate filament to the ophthalmic ganglion. It then gives off the long ciliary nerves, which pass to the ciliary muscle and iris. Its trunk finally divides into the external nasal, or infratrochlearis, and the internal nasal, or ethmoidal. The infratrochlearis is distributed to the integument of the forehead and nose, to the internal surface of the lower eyelid, the lachrymal sac and the caruncula. The internal nasal is distributed to the mucous membrane and also in part to the integument of the nose.

The superior maxillary branch of the fifth passes out of the cranial cavity by the foramen rotundum, traverses the infraörbital canal, and emerges upon the face by the infraörbital foramen. Branches from this nerve are given off in a spheno-maxillary fossa and the infraörbital canal, before it emerges upon the face. In the spheno-maxillary fossa, the first branch is the orbital, which passes into the orbit, giving off one branch, the temporal, which passes through the temporal fossa by a foramen in the malar bone and is distributed to the integument on the temple and the side of the forehead. Another branch, the malar, which likewise emerges by a foramen in the malar bone, is distributed to the integument over this bone. In the spheno-maxillary fossa, are also given off two branches, which pass to the spheno-palatine, or Meckel's ganglion. From this portion of the nerve, branches are given off, the two posterior dental nerves, which are distributed to the molar and bicuspid teeth, the mucous membrane of the corresponding alveolar processes and to the antrum.

In the infraörbital canal, a large branch, the anterior dental, is given off to the teeth and mucous membrane of the alveolar processes not supplied by the posterior dental branches. This branch anastomoses with the posterior dental.

The terminal branches upon the face are distributed to the lower eyelid (the palpebral branches), to the side of the nose (the nasal branches), anastomosing with the nasal branch of the ophthalmic, and to the integument and the mucous membrane of the upper lip (the labial branches).

FIG. 212.—*Inferior maxillary division of the fifth* (Hirschfeld).
1, branch from the motor root to the masseter muscle; 2, filaments from this branch to the temporal muscle; 3, buccal branch; 5, 6, 7, branches to the muscles; 8, *auriculo-temporal nerve*; 9, *temporal branches*; 10, *auricular branches*; 11, *anastomosis with the facial nerve*; 12, *lingual branch*; 13, branch of the motor root to the mylo-hyoid muscle; 14, 15, 15, *inferior dental nerve, with its branches*; 16, *mental branch*; 17, *anastomosis of this branch with the facial nerve.*

The inferior maxillary is a mixed nerve, composed of the inferior division of the large root and the entire small root. The distribution of the motor filaments has already been described. This nerve passes out of the cranial cavity by the foramen ovale, and then separates into the anterior division, containing nearly all of the motor filaments, and the posterior division, which is chiefly sensory. The sensory portion breaks up into the following branches:

1. The auriculo-temporal nerve supplies the integument in the temporal region, the auditory meatus, the integument of the ear, the temporo-maxillary articulation and the parotid gland. It also sends branches of communication to the facial.

2. The lingual branch is distributed to the mucous membrane of the tongue as far as the point, the mucous membrane of the mouth, the gums, and to the sublingual gland. This nerve receives a branch from the facial (the chorda tympani) which has already been described. From this nerve,

also, are given off two or three branches which pass to the submaxillary ganglion.

3. The inferior dental nerve, the largest of the three, passes in the substance of the inferior maxillary bone, beneath the teeth, to the mental foramen, where it emerges upon the face. The most important sensory branches are those which supply the pulps of the teeth and the branches upon the face. The nerve, emerging upon the face by the mental foramen, called the mental nerve, supplies the integument of the chin and the lower part of the face and the lower lip. It also sends certain filaments to the mucous membrane of the mouth.

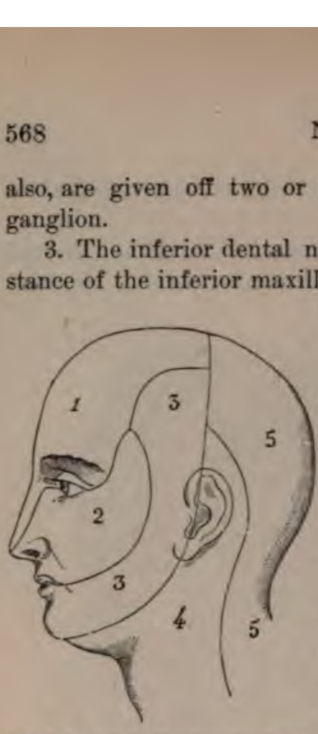



FIG. 213.—*Limits of cutaneous distribution of sensory nerves to the face, head and neck* (Béclard).

1, cutaneous distribution of the ophthalmic division of the fifth; 2, distribution of the superior maxillary division; 3, 3, distribution of the inferior maxillary division; 4, distribution of the anterior branches of the cervical nerves; 5, 5, distribution of the posterior branches of the cervical nerves.

*Properties and Uses of the Trifacial.*—The trifacial is the great sensory nerve of the face and of the mucous membranes lining the cavities about the head. It is impossible to stimulate this nerve at its origin without seriously involving other parts, but all observations with regard to the properties of the large root go to show that it is an exclusively sensory nerve and that its sensibility is very acute as compared with other nerves. It was divided in the cranial cavity by Mayo (1822–'23), Fodéra (1823) and Magendie (1824). Magendie divided the nerve at its root by introducing a small, cutting stylet through the skull. He succeeded in keeping the animals alive for several days or weeks and noted in his experiments immediate loss of sensibility in the face on the side on which the nerve was divided. The operative procedure employed by Magendie has been followed by other physiologists, particularly Bernard, who made a number of important observations on the immediate and remote effects of section of the nerve. The section is usually made through the ganglion of Gasser. The operation is difficult on account of the danger of wounding large blood-vessels. When this operation is performed without accident, the cornea and the integument and mucous membrane upon that side of the head are instantaneously deprived of sensibility and may be pricked, lacerated or burned, without the slightest evidence of pain on the part of the animal. Almost always the small root of the fifth is divided as well as the large root, and the muscles of mastication are paralyzed upon one side; but with this exception, there is no paralysis of motion, sensation alone being destroyed upon one side.

*Immediate Effects of Division of the Trifacial.*—This nerve has never been exposed in the cranial cavity in living animals; but its branches upon the face and the lingual branch of the inferior maxillary division have been operated upon and found to be exquisitely sensitive. Physiologists have exposed the roots in animals immediately after death, and have found that stimulation of the large root carefully insulated produces no muscular contraction. All who have divided this root in living animals must have recognized, not only that it is sensitive, but that its sensibility is far more acute than that of any other nervous trunk in the body.

As far as audition and olfaction are concerned, there are no special effects immediately following section of the trifacial; but there are certain important phenomena observed in connection with the eye and the organs of taste.

At the instant of division of the fifth, the eyeball is protruded and the pupil becomes strongly contracted. This occurs in rabbits, and the contraction of the pupil was observed in the first operations of Magendie. The pupil, however, usually is restored to the normal condition in a few hours. After division of the nerve the lachrymal secretion becomes very much less in quantity; but this is not the cause of the subsequent inflammation, for the eyes are not inflamed, even after extirpation of both lachrymal glands (Magendie). The movements of the eyeball are not affected by division of the fifth.

Another of the immediate effects of complete division of the fifth nerve is loss of general sensibility in the tongue. Most experiments upon the influence of this nerve over the general sensibility and the sense of taste in the tongue have been made by dividing the lingual branch of the inferior maxillary division. When this branch is irritated, there are evidences of intense pain. When it is divided, the general sensibility and the sense of taste are destroyed in the anterior portion of the tongue. It will be remembered, however, that the chorda tympani joins the lingual branch of the fifth as it passes between the pterygoid muscles, and that section of this branch of the facial abolishes the sense of taste in the anterior two-thirds of the tongue. If the gustatory properties of the lingual branch of the fifth be derived from the chorda tympani, lesions of the fifth not involving this nerve would be followed by loss of general sensibility, but the taste would be unaffected. This has been shown to be the fact, by cases of paralysis of general sensibility of the tongue without loss of taste in the human subject, which will be discussed more fully in connection with the physiology of gustation.

Among the immediate effects of section of the fifth, is an interference with the reflex phenomena of deglutition. In a series of observations upon the action of the sensory nerves in deglutition, by Waller and Prevost, it was found that after section of the fifth upon both sides, it was impossible to excite movements of deglutition by stimulating the mucous membrane of the velum palati. After section of the superior laryngeal branches of the pneumogastrics, no movements of deglutition followed stimulation of the mucous membrane of the top of the larynx. In these experiments, when the fifth was divided upon one side, stimulation of the velum upon the corresponding side had no effect, while movements of deglutition were produced by irritating the velum upon the sound side. These experiments show that the fifth nerve is important in the reflex phenomena of deglutition, as a sensory nerve, conveying the impression from the velum palati to the nerve-centres. This action probably takes place through filaments which pass from the fifth to the mucous membrane, through Meckel's ganglion.

*Remote Effects of Division of the Trifacial.*—After section of the fifth nerve in the cranial cavity, the immediate loss of sensibility of the integument and mucous membranes of the face and head is usually supplemented by serious disturbances in the nutrition of the eye, the ear and the mucous membranes of the nose and mouth. After a period varying between a few hours and one or two days after the operation, the eye upon the affected side becomes the seat of purulent inflammation, the cornea becomes opaque and ulcerates, the humors are discharged and the organ is destroyed. Congestion of the parts is usually very prominent a few hours after division of the nerve. At the same time there is an increased discharge from the mucous membranes of the nose and mouth upon the affected side, and ulcers appear upon the tongue and lips. It is probable, also, that disorders in the nutrition of the auditory apparatus follow the operation, although these are not so prominent. Animals affected in this way usually die in fifteen to twenty days.

In the early experiments of Magendie, it was noted that "the alterations in nutrition are much less marked" when the division is effected behind the ganglion of Gasser than when it is done in the ordinary way through the ganglion. It is difficult enough to divide the nerve completely, within the cranium, and is almost impossible to make the operation at will through or behind the ganglion; and the phenomena of inflammation are absent only in exceptional and accidental instances. Magendie offered no satisfactory explanation of the differences in the consecutive phenomena coincident with the place of section of the nerve. The facts, however, have been repeatedly verified. In a number of experiments in which the nerve was divided in the cranial cavity (Flint), the consecutive inflammatory effects were almost always observed; but in an experiment made in 1868, the nerve was completely divided on the left side, as was shown by total loss of sensibility of the parts to which it is distributed, and the animal (a rabbit) lived nearly four months. Four days after the operation the loss of sensibility was still complete. There was very little redness of the conjunctiva of the left eye, and a very slight streak of opacity, so slight that it was distinguished with difficulty. Twelve days after the operation the sensibility of the left eye was distinct but slight. There was no redness of the conjunctiva, and the opacity of the cornea had disappeared. The animal was in good condition, and the line of contact of the upper with the lower incisors, when the jaws were closed, was very oblique. The animal was kept alive by careful feeding with bread and milk for one hundred and seven days after the operation, and there was no inflammation of the organs of special sense. It died at that time of inanition, having become extremely emaciated. The animal never recovered power over the muscles of the left side, and the incisors grew to a great length, interfering very much with mastication.

Longet, in 1842, gave an explanation of the absence of inflammation in certain cases of division of the fifth. He attributed the consecutive inflammation in most experiments to lesion of the ganglion of Gasser and of the sympathetic connections, which are very abundant at this point. These sympathetic filaments are avoided when the section is made behind the ganglion.

The explanation of the phenomena of disordered nutrition in the organs of special sense, particularly the eye, following division of the fifth, is not afforded by the section of this nerve alone; for when the loss of sensibility is complete after division of the nerve behind the Gasserian ganglion, these results may not follow. They are not explained by deficiency in the lachrymal secretion, for they are not observed when both lachrymal glands have been extirpated. They are not due to exposure of the eyeball, for they do not follow section of the facial. They are not due simply to an enfeebled general condition, for in the experiment just detailed, the animal died of inanition after section of the nerve, without any evidences of inflammation. In view of the fact that section of the sympathetic filaments is well known to modify nutrition of parts to which they are distributed, producing congestion, increase in temperature and other phenomena, it is rational to infer that the modifications in nutrition which follow section of the fifth after it receives filaments from the sympathetic system, not occurring when these sympathetic filaments escape division, are to be attributed to lesion of the sympathetic and not to the division of the sensory nerve itself.

A farther explanation is demanded for the inflammatory results which follow division of the sympathetic filaments joining the fifth, inasmuch as division of the sympathetic alone in the neck simply produces exaggeration of the nutritive processes, as evidenced chiefly by local increase in the animal temperature, and not the well-known phenomena of inflammation.

It was remarked by Bernard that the "alterations in nutrition appear more promptly in animals that are enfeebled." Section of the small root of the fifth, which is unavoidable when the nerve is divided within the cranial cavity, generally interferes so much with mastication as to influence seriously the general nutrition; and this might modify the nutritive processes in delicate organs, like the eye, so as to induce those changes which are called inflammatory. The following observation (W. H. Mason) has an important bearing on this question:

The fifth pair of nerves was divided in a cat in the ordinary way. By feeding the animal carefully with milk and finely chopped meat, the nutrition was maintained at a high standard, and no inflammation of the eye occurred for about four weeks. The supply of food was then diminished to about the quantity it would be able to take without any special care, when the eye became inflamed, and perforation of the cornea and destruction of the organ followed. The animal was kept for about five months; at the end of which time, sensation upon the affected side, which had been gradually improving, was completely restored.

The following explains, in a measure at least, the consecutive inflammatory effects of section of the fifth with its communicating sympathetic filaments: By dividing the sympathetic, the eye and the mucous membranes of the nose, mouth and ear are rendered hyperæmic, the temperature probably is raised, and the processes of nutrition are exaggerated. This condition of the parts would seem to require a full supply of nutritive material from the blood, in order to maintain the condition of exaggerated nutrition; but when the blood is impoverished—probably as the result of deficiency in the introduction of nutritive matter, from paralysis of the muscles of mastication upon one side—the nutritive processes in these delicate parts are seriously modified, so as to constitute inflammation. The observation just detailed is an argument in favor of this view; for here the inflammation was arrested when the action of the paralyzed muscles was supplied by careful feeding. With this view, the disorders of nutrition observed after division of the fifth may properly be referred to the sympathetic system.

Pathological facts in confirmation of experiments upon the fifth pair in the lower animals are not wanting; but it must be remembered that in cases of paralysis of the nerve in the human subject, it is not always possible to locate exactly the seat of the lesion and to appreciate fully its extent, as can be done when the nerve is divided by an operation. In studying these cases, it sometimes occurs that the phenomena, particularly those of modified nutrition, are more or less contradictory.

In nearly all works upon physiology, are references to cases of paralysis of the fifth in the human subject. Two cases have been reported by Noyes, in both of which there was inflammation of the eye. In one case the tongue was entirely insensible upon one side, but there was no impairment of the sense of taste. A notable feature in one of the cases was the fact that an operation upon the eyelid of the affected side was performed without the slightest evidence of pain on the part of the patient.

Cases of paralysis of the fifth in the human subject in the main confirm the results of experiments upon the inferior animals. In cases in which the fifth nerve alone is involved in the disease, without the facial, there is simply loss of sensibility upon one side, the movements of the superficial muscles of the face being unaffected. When the small root is involved, the muscles of mastication upon one side are paralyzed; but in certain reported cases in which this root escaped, there was no muscular paralysis. The senses of sight, hearing and smell, except as they were affected by consecutive inflammation, are little if at all disturbed in uncomplicated cases. The sense of taste in the anterior portion of the tongue is perfect, except in those cases in which the facial, the chorda tympani or the lingual branch of the fifth after it had been joined by the chorda tympani is involved in the disease. In some cases there is no alteration in the nutrition of the organs of special sense; but in this respect the facts with regard to the seat of the lesion are not so satisfactory as in experiments upon the lower animals, it being difficult, in most of them, to exactly limit the boundaries of the lesion.

### Pneumogastric (Tenth Nerve).

Of all the nerves emerging from the cranial cavity, the pneumogastric presents the greatest number of anastomoses, the most remarkable course and the most varied uses. Arising from the medulla oblongata by a purely sensory root, it communicates with at least five motor nerves, and it is distributed largely to muscular tissue, both of the voluntary and the involuntary variety.

*Physiological Anatomy.*—The apparent origin of the pneumogastric is from the lateral portion of the medulla oblongata, just behind the olivary body, between the roots of the glosso-pharyngeal and the spinal accessory. The deep origin is mainly from what is called the nucleus of the pneumogastric, in the inferior portion of the gray substance in the floor of the fourth ventricle. The course of the fibres, traced from without inward, is somewhat intricate.

The deep origins of the pneumogastric and glosso-pharyngeal nerves appear to be in the main identical. Tracing the filaments from without inward, they may be followed in four directions: (1) The anterior filaments pass from without inward, first very superficially, in the direction of the olivary body; but they then turn and pass deeply into the substance of the restiform body, in which they are lost. (2) The posterior filaments are superficial, and they pass, with the fibres of the restiform body, toward the cerebellum. (3) Of the intermediate filaments, the anterior pass through the restiform body, the greatest number extending to the median line, in the floor of the fourth ventricle. A few fibres are lost in the middle fasciculi of the medulla and a few pass toward the brain. (4) The posterior intermediate filaments traverse the restiform body, to the floor of the fourth ventricle, when some pass to the median line, and others descend in the substance of the medulla. It is difficult to follow the fibres of origin of the pneumogastrics beyond the median line; but recent observations leave no doubt of the fact that many of these fibres decussate in the floor of the fourth ventricle.

There are two ganglionic enlargements belonging to the pneumogastric. In the jugular foramen, is a well marked, grayish, ovoid enlargement, one-sixth to one-fourth of an inch (4·2 to 6·4 mm.) in length, called the jugular ganglion, or the ganglion of the root. This is united by two or three filaments with the ganglion of the glosso-pharyngeal. It is a true ganglion, containing nerve-cells. After the nerve has emerged from the cranial cavity, it presents on its trunk another grayish enlargement, half an inch to an inch (12 to 25 mm.) in length, called the ganglion of the trunk. This has a plexiform structure, the white fibres being mixed with grayish fibres and nerve-cells. The exit of the nerve from the cranial cavity is by the jugular foramen, or posterior foramen lacerum, in company with the spinal accessory, the glosso-pharyngeal nerve and the internal jugular vein.

*Anastomoses.*—There are occasional filaments of communication which pass from the spinal accessory to the ganglion of the root of the pneumogastric, but these are not constant. After both nerves have emerged from the cranial cavity, an important branch of considerable size passes from the spinal accessory to the pneumogastric, with which it becomes closely united. Experiments have shown that these filaments from the spinal accessory pass in great part to the larynx, by the inferior laryngeal nerves.

In the aquæductus Fallopii, the facial nerve gives off a filament of communication to the pneumogastric, at the ganglion of the root. This filament, joined at the ganglion by sensory filaments from the pneumogastric and some filaments from the glosso-pharyngeal, is called the auricular branch of Arnold. By some anatomists it is regarded as a branch from the facial, and by others it is described with the pneumogastric.

FIG. 214.—*Anastomoses of the pneumogastric* (Hirschfeld).

1, facial nerve; 2, glosso-pharyngeal nerve; 2′, anastomoses of the glosso-pharyngeal with the facial; 3, 3, *pneumogastric, with its two ganglia*; 4, 4, *spinal accessory*; 5, sublingual nerve; 6, superior cervical ganglion of the sympathetic; 7, *anastomotic arcade of the first two cervical nerves*; 8, carotid branch of the superior cervical ganglion of the sympathetic: 9, nerve of Jacobson; 10, branches of this nerve to the sympathetic; 11, branch to the Eustachian tube; 12, branch to the fenestra ovalis; 13, branch to the fenestra rotunda; 14, external deep petrous nerve; 15, internal deep petrous nerve; 16, otic ganglion; 17, *auricular branch of the pneumogastric*; 18, *anastomosis of the pneumogastric with the spinal accessory*; 19, *anastomosis of the pneumogastric with the sublingual*; 20, anastomosis of the spinal accessory with the second pair of cervical nerves; 21, pharyngeal plexus; 22, superior laryngeal nerve.

Two or three small filaments of communication pass from the sublingual to the ganglion of the trunk of the pneumogastric.

At the ganglion of the trunk, the pneumogastric generally receives filaments of communication from the arcade formed by the anterior branches of the first two cervical nerves. These, however, are not constant.

The pneumogastric is connected with the sympathetic system by a number of filaments of communication from the superior cervical ganglion, passing in part upward toward the ganglion of the root of the pneumogastric, and in part transversely and downward. These filaments frequently are short, and they bind the sympathetic ganglion to the trunk of the nerve. The main trunk of the pneumogastric and its branches receive a few filaments of communication from the middle and inferior cervical and the upper dorsal ganglia of the sympathetic.

The pneumogastric frequently sends a slender filament to the glosso-pharyngeal nerve, at or near the ganglion of Andersch. Branches from the pneumogastric join branches from the glosso-pharyngeal, the spinal accessory and the sympathetic, to form the pharyngeal plexus.

*Distribution.*—Although the pneumogastric nerves upon the two sides do not present any important differences in the destination of their filaments, as far down as the diaphragm, the distribution of the abdominal branches is not the same. The most important branches are the following:

1. Auricular.
2. Pharyngeal.
3. Superior laryngeal.
4. Inferior, or recurrent laryngeal.
5. Cardiac, cervical and thoracic.
6. Pulmonary, anterior and posterior.
7. Œsophageal.
8. Abdominal.

The auricular nerves are sometimes described in connection with the facial. They are given off from the ganglion of the trunk of the pneumogastric and are composed of filaments of communication from the facial and from the glosso-pharyngeal, as well as of filaments from the pneumogastric itself. The nerves thus constituted are distributed to the integument of the upper portion of the external auditory meatus, and a small filament is sent to the membrana tympani.

FIG. 215.—*Distribution of the pneumogastric* (Hirschfeld).

1, *trunk of the left pneumogastric*; 2, *ganglion of the trunk*; 3, *anastomosis with the spinal accessory*; 4, *anastomosis with the sublingual*; 5, *pharyngeal branch* (*the auricular branch is not shown in the figure*); 6, *superior laryngeal branch*; 7, *external laryngeal nerve*; 8, *laryngeal plexus*; 9, 9, *inferior laryngeal branch*; 10, *cervical cardiac branch*; 11, *thoracic cardiac branch*; 12, 13, *pulmonary branches*; 14, lingual branch of the fifth; 15, lower portion of the sublingual; 16, glosso-pharyngeal; 17, spinal accessory; 18, 19, 20, spinal nerves; 21, phrenic nerve; 22, 23, spinal nerves; 24, 25, 26, 27, 28, 29, 30, sympathetic ganglia.

The pharyngeal nerves are given off from the superior portion of the ganglion of the trunk, and they contain a large number of the filaments of communication which the pneumogastric receives from the spinal accessory. In their course by the sides of the superior constrictor muscles of the pharynx, these nerves anastomose with filaments from the glosso-pharyngeal and the superior cervical ganglion of the sympathetic, to form what is known as the pharyngeal plexus. The ultimate filaments of distribution pass to the muscles and the mucous membrane of the pharynx. Physiological experiments have shown that the motor influence transmitted to the pharyngeal muscles through the pharyngeal branches of the pneumogastric is derived from the spinal accessory.

The superior laryngeal nerves are given off from the lower part of the ganglion of the trunk. Their filaments come from the side opposite to the point of junction of the pneumogastric with the communicating branch from the spinal accessory, so that probably the superior laryngeals contain few if any motor fibres from the eleventh nerve. The superior laryngeal gives off the external laryngeal, a long, delicate branch, which sends a few filaments to the inferior constrictor of the pharynx and is distributed to the crico-thyroid muscle and the mucous membrane of the ventricle of the larynx. The external laryngeal branch anastomoses with the inferior laryngeal nerve and with the sympathetic. The internal branch is distributed to the mucous membrane of the epiglottis, the base of the tongue, the aryteno-epiglottidean fold and the mucous membrane of the larynx as far down as the true vocal chords. A branch from this nerve, in its course to the larynx, penetrates the arytenoid muscle, to which it sends a few filaments, but these are all sensory. This branch also supplies the crico-thyroid muscle. It anastomoses with the inferior laryngeal nerve. An important branch, described by Cyon and Ludwig, in the rabbit, under the name of the depressor-nerve, arises by two roots, one from the superior laryngeal and the other from the trunk of the pneumogastric. It passes down the neck by the side of the sympathetic, and in the chest, it joins filaments from the thoracic sympathetic, to pass to the heart, between the aorta and the pulmonary artery. This nerve is not isolated in the human subject, but it is probable that analagous fibres exist in man in the trunk of the pneumogastric.

It is important from a physiological point of view to note that the superior laryngeal nerve is the nerve of sensibility of the upper part of the larynx, as well as of the supralaryngeal mucous membranes, and that it animates a single muscle of the larynx (the crico-thyroid) and the inferior constrictor of the pharynx.

The inferior, or recurrent laryngeal nerves present some slight differences in their anatomy upon the two sides. Upon the left side the nerve is the larger and is given off at the arch of the aorta. Passing beneath this vessel, it ascends in the groove between the trachea and the œsophagus. In its upward course it gives off certain filaments which join the cardiac branches, filaments to the muscular tissue and mucous membrane of the upper part of the œsophagus, filaments to the mucous membrane and the intercartilaginous muscular tissue of the trachea, one or two filaments to the inferior constrictor of the pharynx and a branch which joins the superior laryngeal. Its terminal branches penetrate the larynx, behind the posterior articulation of the thyroid with the cricoid cartilage, and are distributed to all of the intrinsic muscles of the larynx, except the crico-thyroids, which are supplied by the superior laryngeal. Upon the right side the nerve winds from before backward around the subclavian artery, and it has essentially the same course and distribution as upon the left side, except that it is smaller and has fewer filaments of distribution.

The important physiological point connected with the anatomy of the recurrent laryngeals is that they animate all of the intrinsic muscles of the larynx, except the crico-thyroid. Experiments have shown that these nerves contain a large number of motor filaments derived from the spinal accessory.

The cervical cardiac branches, two or three in number, arise from the pneumogastrics at different points in the cervical portion, and pass to the cardiac plexus, which is formed in great part of filaments from the sympathetic. The thoracic cardiac branches are given off from the pneumogastrics, below the origin of the inferior laryngeals, and join the cardiac plexus.

The anterior pulmonary branches are few and delicate as compared with the posterior branches. They are given off below the origin of the thoracic cardiac branches, send a few filaments to the trachea, and then form a plexus which surrounds the bronchial tubes and follows the bronchial tree to its terminations in the air-cells. The posterior pulmonary branches are larger and more abundant than the anterior. They communicate freely with sympathetic filaments from the upper three or four thoracic ganglia and then form the great posterior pulmonary plexus. From this plexus a few filaments go to the inferior and posterior portion of the trachea, a few pass to the muscular tissue and mucous membrane of the middle portion of the œsophagus, and a few are sent to the posterior and superior portion of the pericardium. The plexus then surrounds the bronchial tree and passes with its ramifications to the pulmonary tissue, like the corresponding filaments of the anterior branches. The pulmonary branches are distributed to the mucous membrane, and not to the walls of the blood-vessels.

The œsophageal branches take their origin from the pneumogastrics, above and below the pulmonary branches. These branches from the two sides join to form the œsophageal plexus, their filaments of distribution going to the muscular tissue and the mucous membrane of the lower third of the œsophagus.

The abdominal branches are quite different in their distribution upon the two sides.

Upon the left side the nerve, which is here anterior to the cardiac opening of the stomach, immediately after its passage by the side of the œsophagus into the abdomen, divides into a number of branches, which are distributed to the muscular walls and the mucous membrane of the stomach. As the branches pass from the lesser curvature, they take a downward direction and go to the liver, and with another branch running between the folds of the gastro-hepatic omentum, they follow the course of the portal vein in the hepatic substance. The branches of this nerve anastomose with the nerve of the right side and with the sympathetic.

The right pneumogastric, situated posteriorly, at the œsophageal opening of the diaphragm, sends a few filaments to the muscular coat and the mucous membrane of the stomach, passes backward and is distributed to the liver, spleen, kidneys, suprarenal capsules and finally to the whole of the small intestine (Kollmann). The anatomical researches by Kollmann (1860) have been fully confirmed by physiological experiments. Before the nerves pass to the intestines, there is a free anastomosis and interchange of filaments between the right and the left pneumogastric.

*General Properties of the Roots of Origin of the Pneumogastrics.*—The sensibility of the pneumogastrics in the neck, while it is dull as compared with the properties of other sensory nerves, is nevertheless distinct. It is impossible, however, to expose the roots of the nerves in living animals, before they have received communicating motor filaments, without such mutilation as would interfere with accurate observations; but in animals just killed, if the roots be exposed and divided, so as to avoid reflex movements, and if care be taken to avoid stimulation of motor filaments from adjacent nerves, it is found that the application of electricity to the peripheral end of the root, from its origin to the ganglion, gives rise to no movements. It may therefore be assumed that the true filaments of origin of the pneumogastrics are exclusively sensory or at least that they have no motor properties.

*Properties and Uses of the Auricular Nerves.*—There is very little to be said with regard to the auricular nerves after a description of their anatomy. They are sometimes described with the facial and sometimes with the pneumogastric. They contain filaments from the facial, the pneumogastric and the glosso-pharyngeal. The sensory filaments of these nerves give sensibility to the upper part of the external auditory meatus and the membrana tympani.

*Properties and Uses of the Pharyngeal Nerves.*—The pharyngeal branches of the pneumogastric are mixed nerves, their motor filaments being derived from the spinal accessory; and their direct action upon the muscles of deglutition belongs to the physiological history of the last-named nerve. As already stated in treating of the spinal accessory, the filaments of communication that go to the pharyngeal branches of the pneumogastric are distributed to the pharyngeal muscles.

It is impossible to divide all of the pharyngeal filaments in living animals and observe directly how far the general sensibility of the pharynx and the reflex phenomena of deglutition are influenced by this section. As far as one can judge from the distribution of the filaments to the mucous membrane, it would seem that they combine with the pharyngeal filaments of the fifth, and possibly with sensory filaments from the glosso-pharyngeal, in giving general sensibility to these parts.

In the experiments of Waller and Prevost, upon the reflex phenomena of deglutition, it is shown that the action of the pharyngeal muscles can not be excited by stimulation of the mucous membrane of the supralaryngeal region and the pharynx, after section of the fifth and of the superior laryngeal branches of the pneumogastrics. This would seem to show that the pharyngeal branches of the pneumogastrics are of little importance in these reflex phenomena.

*Properties and Uses of the Superior Laryngeal Nerves.*—The stimulation of these nerves produces intense pain and contraction of the crico-thyroids; but it has been shown by experiment that the arytenoid muscles, through which the nerves pass, receive no motor filaments. The influence of the nerves upon the muscles resolves itself into the action of the crico-thyroids, which has been treated of fully under the head of phonation. When these muscles are paralyzed, the voice becomes hoarse. The filaments to the inferior muscles of the pharynx are few and comparatively unimportant. The superior laryngeals do not receive their motor filaments from the spinal accessory.

The sensory filaments of the superior laryngeals have important uses connected with the protection of the air-passages from the entrance of foreign matters, particularly in deglutition, and they are also concerned in the reflex action of the constrictors of the pharynx. When both superior laryngeals have been divided in living animals, liquids often pass in small quantity into the larynx, owing to the absence of the reflex closure of the glottis when foreign matters are brought in contact with its superior surface and the occasional occurrence of inspiration during deglutition.

Aside from the protection of the air-passages, the superior laryngeal is one of the sensory nerves through which the reflex acts in deglutition operate. There are certain parts which depend for their sensibility entirely upon this nerve; viz., the mucous membrane of the epiglottis, of the aryteno-epiglottidean fold and of the larynx as far down as the true vocal chords. When an impression is made upon these parts, as when they are touched with a piece of meat, regular and natural movements of deglutition ensue.

If the superior laryngeal nerves be divided and a stimulus be applied to their central ends, movements of deglutition are observed, and there is also arrest of the action of the diaphragm. From these experiments, it would seem that the impression which gives rise to the movements of deglutition aids in protecting the air-passages from the entrance of foreign matters, by temporarily arresting the inspiratory act.

*Properties and Uses of the Inferior, or Recurrent Laryngeal Nerves.*—The anatomical distribution of these nerves shows that their most important action is connected with the muscles of the larynx. The few filaments which are given off in the neck, to join the cardiac branches, are probably not very important. It is proper to note, however, that the inferior laryngeal nerves supply the muscular tissue and mucous membrane of the upper part of the œsophagus and trachea, and one or two branches are sent to the inferior constrictor of the pharynx. The action of these filaments is sufficiently evident.

The inferior laryngeals contain chiefly motor filaments, as is evident from their distribution as well as from the effects of direct stimulation. All who have experimented upon these nerves have noted little or no evidence of pain when they are irritated or divided.

One of the most important uses of the recurrents relates to the production of vocal sounds. In connection with the physiology of the internal, or communicating branch from the spinal accessory to the pneumogastric, it has been shown that this branch of the spinal accessory is the true nerve of phonation. Before the uses of the spinal accessory were fully understood, the experiments upon the inferior laryngeals led to the opinion that these were the nerves of phonation, as loss of voice follows their division in living animals. It is true that these nerves contain the filaments which preside over the vocal movements of the larynx; but it is also the fact that these vocal filaments are derived exclusively from the spinal accessory, and that the recurrents contain as well motor filaments which preside over movements of the larynx not concerned in the production of vocal sounds.

The muscles of the larynx concerned in phonation are the crico-thyroids, animated by the superior laryngeals, and the arytenoid, the lateral crico-arytenoids and the thyro-arytenoids, animated by the inferior laryngeals. The posterior crico-arytenoids are respiratory muscles, and these are not affected by extirpation of the spinal accessories, but the glottis is still capable of dilatation, so that inspiration is not impeded. If, however, the spinal accessories be extirpated and the larynx be then exposed in a living animal, the glottis still remains dilated, but will not close when irritated. If the inferior laryngeals be then divided, the glottis is mechanically closed with the inspiratory act, and the animals often die of suffocation. In view of the varied sources from which the pneumogastrics receive their motor filaments, it is easy to understand how certain of these may preside over the vocal movements, and others, from a different source, may animate the respiratory movements.

The impediment to the entrance of air into the lungs is a sufficient explanation of the increase in the number of the respiratory acts after division of both recurrents. The acceleration of respiration is much greater in young than in adult animals. This does not apply to very young animals, in which section of the recurrents produces almost instant death.

Feeble stimulation of the central ends of the inferior laryngeals, after their division, produces rhythmical movements of deglutition, generally coincident with arrest of the action of the diaphragm. These phenomena are generally observed in rabbits, but they are not constant. The reflex action of these nerves in deglutition probably is dependent upon the communicating filaments which they send to the superior laryngeal nerves.

*Properties and Uses of the Cardiac Nerves.*—The chief uses of the cardiac branches relate to the influence of the pneumogastrics on the action of the heart. This has already been considered in connection with the physiology of the circulation. The effect of dividing the pneumogastrics in the neck is to remove the heart from the influence of its inhibitory nerves; but at the same time, the operation profoundly affects the respiratory movements, and this latter effect must be eliminated as far as possible in studying the influence of the pneumogastrics on the circulation. The same remark applies to the experiment of Faradization of the pneumogastrics in the neck. The cardiac branches are operated upon with difficulty, and most experiments have been made upon the cervical portion of the pneumogastric itself.

Faradization of the pneumogastrics in the neck arrests the action of the heart in diastole (the brothers Weber, 1846). This is a direct action and is due to the excitation of the inhibitory fibres, which are derived from the spinal accessory nerves. The phenomena following stimulation of these nerves have already been described in connection with the physiology of the circulation and the properties and uses of the spinal accessories.

*Depressor Nerve.*—While this nerve, which has been described in the rabbit (Cyon and Ludwig, 1867), is not isolated in the human subject, it is probable that fibres, the action of which is analogous to the action observed in animals in which the nerve is anatomically distinct, exist in the trunk of the pneumogastric. The action of the depressor nerves, which is reflex, has already been described in connection with the physiology of the circulation.

*Properties and Uses of the Pulmonary Nerves.*—The trachea, bronchia and the pulmonary structure are supplied with motor and sensory filaments by branches of the pneumogastrics. The recurrent laryngeals supply the upper part, and the pulmonary branches, the lower part of the trachea, the lungs themselves being supplied by the pulmonary branches alone. The sensibility of the mucous membrane of the trachea and bronchia is due to the pneumogastrics, for these parts are insensible to irritation when the nerves have been divided in the neck. Longet has shown that while an animal coughed and showed signs of pain when the mucous membrane of the respiratory passages was irritated, after division of the pneumogastrics there was no evidence of sensibility, even when the tracheal mucous membrane was treated with strong acid or cauterized. He also saw the muscular fibres of the small bronchial tubes contract when an electric stimulus was applied to the branches of the pneumogastrics.

*Effects of Division of the Pneumogastrics upon Respiration.*—Section of both pneumogastrics in the neck, in mammals and birds, is usually followed by death, in two to five days. In very young animals, death may occur almost instantly from paralysis of the respiratory movements of the glottis. It has been found by all experimenters that animals survived and presented no very distinct abnormal phenomena after section of one nerve. According to Longet, animals operated upon in this way present hoarseness of the voice and a slight increase in the number of respiratory acts. Some observers have found the corresponding lung partly emphysematous and partly engorged with blood, and others have not noted any change in the pulmonary structure.

When both nerves are divided in full-grown dogs, the effect upon the respiratory movements is very marked. For a few seconds the number of respiratory acts may be increased; but so soon as the animal becomes tranquil, the number is very much diminished and the movements change their character. The inspiratory acts become unusually profound and are attended with excessive dilatation of the thorax. The animal generally is quiet and indisposed to move. Under these conditions the number of respirations may fall from sixteen or eighteen to four per minute.

In most animals that die from section of both pneumogastrics, the lungs are found engorged with blood, and, as it were, carnified, so that they sink in water. This condition is not the result of inflammation of the pulmonary parenchyma, although this was the view formerly entertained and is even now held by some physiologists. Bernard found that the pulmonary lesion did not exist in birds, although section of both nerves was fatal. It had previously been ascertained that in some animals death takes place with no alteration of the lungs. When the entrance of the secretions into the air passages was prevented by the introduction of a canula into the trachea, the solidification of the lungs was nevertheless observed. Without detailing all of the experiments upon which the explanation offered by Bernard is based, it is sufficient to state that he observed a traumatic emphysema as a consequence of the excessively labored and profound inspirations. Indeed, this can be actually seen when the pleura is exposed in living animals. As a result of this excessive distention of the air-cells, the pulmonary capillaries are ruptured in different parts, the blood becomes coagulated and the lungs are finally solidified. This can not occur in birds, because the lungs are fixed, and their relations are such that they are not exposed to excessive distention in inspiration.

The pneumogastrics sometimes reunite after division. The following observation (Flint, 1874) illustrates this fact, which has frequently been noted: Both pneumogastrics were divided in the neck in a medium-sized dog. The pulse was immediately increased from one hundred and twenty to two hundred and forty in the minute, and the number of respirations fell from twenty-four to four or six. In ten days the pulse and respirations had become normal. The dog was then killed by section of the medulla oblongata, and the reunion of the divided ends of the nerves was found to be nearly complete.

The relations of the pneumogastrics to the respiratory nervous centre have been fully considered in connection with the physiology of respiration.

*Effects of Faradization of the Pneumogastrics upon Respiration.*—Faradization of the pneumogastrics in the neck, if the current be sufficiently powerful, arrests respiration. This arrest may be produced at any time with reference to the respiratory act, either in expiration or inspiration, although it is more readily effected in expiration. During the passage of the current the general movements of the animal are also arrested. Although respiration may always be arrested in this way, quite a powerful current is required. During the passage of a very feeble current, the respirations are accelerated. They are then retarded as the current is made stronger, until they finally cease (Bert).

The following are the phenomena, observed by Bert, during the passage of a powerful Faradic current:

"If an excitation be employed sufficiently powerful to arrest respiration in inspiration, all respiratory movements may be made to cease at the very moment when the excitation is applied (inspiration, half-inspiration, expiration), either by operating upon the pneumogastric, or operating upon the laryngeal. . . .

"Any feeble excitation of centripetal nerves increases the number of the respiratory movements; any powerful excitation diminishes them. A powerful excitation of the pneumogastrics, of the superior laryngeal, of the nasal branch of the infraörbital, may arrest them completely; if the excitation be sufficiently energetic, the arrest takes place at the very moment it is applied. Finally, sudden death of the animal may follow a too powerful impression thus transmitted to the respiratory centre: all this being true for certain mammalia, birds and reptiles."

The above expresses the most important experimental facts at present known with regard to the influence of stimulation of the pneumogastrics upon respiration. The pulmonary branches themselves are so deeply situated that they have not as yet been made the subject of direct experiment, with any positive and satisfactory results.

*Properties and Uses of the Œsophageal Nerves.*—The muscular walls and the mucous membrane of the œsophagus are supplied entirely by branches from the pneumogastrics. The upper portion is supplied by filaments from the inferior laryngeal branches, the middle portion, by filaments from the posterior pulmonary branches, and the inferior portion receives the œsophageal branches. These branches are both sensory and motor; but probably the motor filaments largely predominate, for the mucous membrane, although it is sensible to the extremes of heat and cold, the feeling of distention, and a burning sensation upon the application of strong irritants, is by no means acutely sensitive.

That the movements of the œsophagus are animated by branches from the pneumogastrics, has been clearly shown by experiments. In the first place, except in animals in which the anatomical distribution of the nerves is different from the arrangement in the human subject, the entire œsophagus is paralyzed by dividing the nerves in the neck. When the pneumogastrics are divided in the cervical region in dogs, if the animals attempt to swallow a considerable quantity of food, the upper part of the œsophagus is found enormously distended. Bernard noted in a dog in which a gastric fistula had been established, that articles of food given to the animal did not pass into the stomach, although he made great efforts to swallow. An instant after the attempt, the matters were regurgitated, mixed with mucus, but of course did not come from the stomach.

Direct experiments upon the roots of the pneumogastrics have shown that these nerves influence the movements of the œsophagus, and that the motor filaments involved do not come from the spinal accessory; but it is not known from what nerves these motor filaments are derived.

*Properties and Uses of the Abdominal Nerves.*—In view of the extensive distribution of the terminal branches of the pneumogastrics to the abdominal organs, it is evident that the action of these nerves must be very important, particularly since it has been shown that the right nerve is distributed to the whole of the small intestine.

*Influence of the Pneumogastrics upon the Liver.*—There is very little known with regard to the influence of the pneumogastrics upon the secretion of bile; and the most important experiments upon the innervation of the liver relate to the production of glycogen. If both pneumogastrics be divided in the neck, and if the animal be killed at a time varying between a few hours and one or two days after, the liver contains no sugar, under the conditions in which it is generally found; viz., a certain time after death. From experiments of this kind, Bernard concluded that the glycogenic processes are suspended when the nerves are divided. The experiments, however, made by irritating the pneumogastrics, were more satisfactory, as in these he looked for sugar in the blood and in the urine and did not confine his examinations for sugar to the substance of the liver.

After division of pneumogastrics in the neck, if the peripheral ends be stimulated there is no effect upon the liver; but if the stimulus be applied to the central ends, the glycogenic processes become exaggerated, and sugar makes its appearance in the blood and in the urine. Bernard made a number of experiments illustrating this point, upon dogs and rabbits. The current employed was generally feeble, and it was continued for five or ten minutes, two or three times in an hour. In some instances the stimulation was kept up for thirty minutes. From these experiments, it is assumed that the physiological production of glycogen by the liver is reflex and is due to an impression conveyed to the nerve-centres through the pneumogastrics. The inhalation of irritating vapors and of anæsthetics produces an increased glycogenic action in the liver.

The effects of irritating the floor of the fourth ventricle, by which temporary diabetes is produced, have been considered in connection with the glycogenic action of the liver. This effect is not due to a direct transmission of the irritation to the liver through the pneumogastrics, for the phenomena are observed in animals upon which this operation has been performed after section of both pneumogastrics in the neck. It is probable, indeed, that the impression is conveyed to the liver through the sympathetic system; for it has been shown that animals do not become diabetic after irritation of the floor of the fourth ventricle when the branches of the sympathetic going to the solar plexus have been divided. The operation, however, of dividing the sympathetic nerves in this situation is so serious, that it may interfere with the experiment in some other way than by the direct influence of the nerves upon the liver.

*Influence of the Pneumogastrics upon the Stomach and Intestines.*—Little or nothing is known with regard to the action of the pneumogastrics on the spleen, kidneys and suprarenal capsules. The influence of these nerves upon the stomach and intestine will be considered under the following heads:

1. The effects of Faradization of the nerves.
2. The effects of section of the nerves upon the movements of the stomach in digestion.
3. The influence of the nerves upon the small intestine.

*Effects of Faradization.*—The stomach contracts under stimulation of the pneumogastrics in the neck, not instantly, but after the lapse of five or six seconds (Longet). Longet explained some of the contradictory results obtained by other observers by the fact that these contractions are very marked during stomach-digestion, while they are wanting "when the stomach is entirely empty, retracted on itself and in a measure in repose." Stimulation of the splanchnic nerves, while it produces movements of the intestines, does not affect the stomach. Judging from the tardy contraction of the stomach and the analogy between the action of the pneumogastrics upon this organ and the action of the sympathetic nerves upon the non-striated muscular tissue, Longet assumed that the motor action of the pneumogastrics is due, not to the proper filaments of these nerves, but to filaments derived from the sympathetic.

*Effects of Section of the Pneumogastrics upon the Movements of the Stomach.*—If the pneumogastrics be divided in the neck in a dog in full digestion, in which a gastric fistula has been established so that the interior of the organ can be explored, the following phenomena are observed:

In the first place, before division of the nerves, the mucous membrane of the stomach is turgid, its reaction is intensely acid, and if the finger be introduced through the fistula, it will be firmly grasped by the contractions of the muscular walls. When the pneumogastrics are divided, the contractions of the muscular walls instantly cease, the mucous membrane becomes pale, the secretion of gastric juice is apparently arrested and the sensibility of the organ is abolished (Bernard).

Notwithstanding the apparent arrest of the movements of the stomach in digestion, by section of the pneumogastrics, it has been shown that substances may be very slowly passed to the pylorus, and that the movements, although they are greatly diminished in activity, are not entirely abolished. This fact has been established by the experiments of Schiff, who attributed the movements occurring after section of the nerves to local irritation of the intramuscular terminal nervous filaments.

The influence of the pneumogastrics upon the general processes of digestion, the sensations of hunger and thirst and upon absorption from the alimentary canal have already been considered in connection with the physiology of digestion and absorption.

*Influence of the Pneumogastrics upon the Small Intestine.*—Physiologists have given but little attention to the influence of the pneumagastrics upon the intestinal canal, for the reason that the distribution of the abdominal branches to the small intestine, notwithstanding the researches of Kollmann, in 1860, does not appear to have been generally recognized. The right, or posterior abdominal branch was formerly supposed to be lost in the semilunar ganglion and the solar plexus, after sending a few filaments to the stomach; but since it has been shown that this nerve is supplied to the whole of the small intestine, its physiology, in connection with intestinal secretion, has assumed considerable importance.

The experiments of Wood have shown that the pneumogastrics influence intestinal as well as gastric secretion. After section of the nerves in the cervical region, the most powerful cathartics (croton-oil, calomel, podophyllin, jalap, arsenic etc.), fail to produce purgation, even in doses sufficient to cause death. The articles used were either given by the mouth, just before dividing the nerves, or were injected under the skin.

Although the observations of Wood are not entirely new, they are by far the most extended and satisfactory, and were made with a knowledge of the fact of the distribution of the nerves to the small intestine. Brodie failed to produce purging in dogs, when both pneumogastrics had been divided in the neck, after the administration of arsenic by the mouth and after injecting it under the skin. Reid made five experiments, and in all but one, it is stated that diarrhœa existed after division of the nerves. In twenty experiments by Wood, there was no purgation after division of the nerves, in one there was free purgation, and in one there was "some slight muco-fæcal discharge." From these, Wood concluded that while section of the cervical pneumogastrics, in the great majority of instances, arrests gastro-intestinal secretion and prevents the action of purgatives upon the intestinal canal, a few exceptional cases occur in which these effects are not observed.

It would be interesting to determine whether the pneumogastrics influence the intestinal secretions through their own fibres or through filaments received from the sympathetic system; but there are no experimental facts sufficiently definite to admit of a positive answer to this question. If the action take place through the sympathetic system, as in the case of the stomach, the filaments of communication join the pneumogastrics high up in the neck.

The cranial nerves that have been considered in this chapter are the third, fourth, fifth, sixth, seventh, tenth, eleventh and twelfth. The anatomical and physiological history of the olfactory (first), optic (second), auditory (eighth), gustatory (branch of the seventh and a part of the ninth) and of the general sensory nerves, as far as they are concerned in the sense of touch, belongs properly to the chapters on the special senses.

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# CHAPTER XVIII.

## *THE SPINAL CORD.*

General arrangement of the cerebro-spinal axis—Membranes of the encephalon and spinal cord—Cephalo-rachidian fluid—Physiological anatomy of the spinal cord—Columns of the Cord—Direction of the nerve-fibres in the cord—General properties of the spinal cord—Motor paths in the cord—Sensory paths in the cord—Relations of the posterior white columns of the cord to muscular co-ordination—Nerve-centres in the spinal cord—Reflex action of the spinal cord—Exaggeration of reflex excitability by decapitation, poisoning with strychnine etc.—Reflex phenomena observed in the human subject.

THE nervous matter contained in the cavity of the cranium and in the spinal canal, exclusive of the roots of the cranial and spinal nerves, is known as the cerebro-spinal axis. This portion of the nervous system is composed of white and gray matter. The fibres of the white matter act solely as conductors. The gray matter constitutes a chain of ganglia, which act as nerve-centres, receiving impressions and generating the so-called nerve-force. Certain parts of the gray matter also serve as conductors.

The cerebro-spinal axis is enveloped in membranes, which are for its protection and for the support of its nutrient vessels. It is surrounded to a certain extent with liquid, and it presents cavities, as the ventricles of the brain and the central canal of the cord, which contain liquid. The gray matter is distinct from the white, even to the naked eye. In the spinal cord the white substance is external and the gray is internal. The surface of the brain presents an external layer of gray matter, the white substance being internal. In the white substance of the brain, also, are collections of gray matter. The white matter of the cerebro-spinal axis is composed largely of fibres. The gray substance is composed chiefly of cells.

The encephalon is contained in the cranial cavity and consists of the cerebrum, cerebellum, pons Varolii and medulla oblongata. In the human subject and in many of the higher animals, its surface is marked by convolutions, by which the extent of its gray substance is much increased. The cerebrum, the cerebellum and most of the encephalic ganglia are connected with the white substance of the encephalon and with the spinal cord. All of the cerebro-spinal nerves are connected with the encephalon and the cord. The cerebro-spinal axis acts as a conductor, and its different collections of gray matter, or ganglia, receive impressions conveyed by the sensory conducting fibres, and generate motor impulses which are transmitted to the proper organs by the motor fibres.

*Membranes of the Encephalon and Spinal Cord.*—The membranes of the brain and spinal cord are the dura mater, the arachnoid and the pia mater.

The dura mater of the encephalon is a dense membrane, in two layers, composed chiefly of ordinary fibrous tissue, which lines the cranial cavity and is adherent to the bones. In certain situations its two layers are separated and form what are known as the venous sinuses. The dura mater also sends off folds or processes of its internal layer. One of these passes into the longitudinal fissure and is called the falx cerebri; another lies between the cerebrum and the cerebellum and is called the tentorium; another is situated between the lateral halves of the cerebellum and is called the falx cerebelli. The dura mater is closely attached to the bone at the border of the foramen magnum. From this point it passes into the spinal canal and forms a loose covering for the cord. In the spinal canal, this membrane is not adherent to the bones, which have, like most other bones in the body, a special periosteum. At the foramina of exit of the cranial and the spinal nerves, the dura mater sends out processes which envelop the nerves, with the fibrous sheaths of which they soon become continuous.

The arachnoid is a delicate membrane, resembling the serous membranes, with the exception that it presents but one layer. Its inner surface is covered with a layer of tesselated endothelium. There is a considerable quantity of liquid between the arachnoid and the pia mater, surrounding the cerebro-spinal axis, in what is called the subarachnoid space. This is called the cerebro-spinal, or cephalo-rachidian fluid. The arachnoid does not follow the convolutions and fissures of the encephalon or the fissures of the cord, but it simply covers their surfaces. Magendie described a longitudinal, incomplete, cribriform, fibrous septum in the cord, passing from the inner layer of the arachnoid to the pia mater. A similar arrangement is found in certain situations at the base of the skull.

The pia mater of the encephalon is a delicate, fibrous structure, very vascular, seeming to present, indeed, only a skeleton net-work of fibres for the support of the vessels going to the nervous substance. This membrane covers the surface of the encephalon immediately, follows the sulci and fissures, and is prolonged into the ventricles, where it forms the choroid plexus and the velum interpositum. From its internal surface small vessels are given off which pass into the nervous substance.

The pia mater of the encephalon is continuous with the corresponding membrane of the cord; but in the spinal canal the membrane is thicker, stronger, more closely adherent to the subjacent parts, and its blood-vessels are not so abundant. In this situation many of the fibres are arranged in longitudinal bands. This membrane lines the anterior fissure and a portion of the posterior fissure of the cord. At the foramina of exit of the cranial and the spinal nerves, the fibrous structure of the pia mater becomes continuous with the nerve-sheaths.

Between the anterior and posterior roots of the spinal nerves, on either side of the cord, is a narrow, ligamentous band, the ligamentum denticulatum, which assists in holding the cord in place. This extends from the foramen magnum to the terminal filament of the cord, and is attached, internally, to the pia mater, and externally, to the dura mater.

It is not necessary to enter into a detailed description of the arrangement of the blood-vessels, nerves and lymphatics of the membranes of the brain and spinal cord, or of the vascular arrangement in the substance of the cerebro-spinal axis, as these points are chiefly of anatomical interest. The circulation in these parts presents certain peculiarities. In the first place, the encephalon being contained in an air-tight case of invariable capacity, it has been a question whether or not the vessels be capable of contraction and dilatation, or whether the quantity of blood in the brain be subject to modifications in health or disease. These questions may certainly be answered in the affirmative. In infancy and in the adult, when an opening has been made in the skull, the volume of the encephalon is evidently increased during expiration and is diminished in inspiration. Under normal conditions, in the adult, it is probable that the quantity of blood is increased in expiration and diminished in inspiration; but it is not probable that the cerebro-spinal axis undergoes any considerable movements. The important peculiarities in the cerebral circulation have already been fully considered in connection with the physiology of the circulation. It has been shown that the encephalic capillaries are surrounded or nearly surrounded by canals (perivascular canal-system), which are connected with lymphatic trunks or reservoirs situated under the pia mater. The system of canals may, by variations in its contents, serve to equalize the quantity of liquid in the brain, as the blood-vessels are distended or contracted.

*Cephalo-Rachidian Fluid.*—The greatest part of the fluid in the cranium and in the spinal canal is contained in the subarachnoid space. The ventricles of the encephalon are in communication with the central canal of the cord, and are also connected with the general subarachnoid space, by a narrow, triangular orifice situated at the inferior angle of the fourth ventricle. By this arrangement the liquid in the ventricles of the encephalon and in the central canal of the cord communicates with the liquid surrounding the cerebro-spinal axis, and the pressure upon these parts is equalized.

As far as is known, the office of the cephalo-rachidian fluid is simply mechanical, and its properties and composition have no very definite physiological significance. Its quantity was estimated by Magendie, in the human subject, at about two fluidounces (60 c. c.); but this was the smallest quantity obtained by placing the subject upright, making an opening in the lumbar region and a counter-opening in the head to admit the pressure of the atmosphere. The exact quantity in the living subject could hardly be estimated in this way; and it is difficult, indeed, to see how any thing more than a roughly approximate idea could be obtained. The quantity obtained by Magendie probably does not represent all the liquid contained in the ventricles and in the subarachnoid space, but it is the most definite estimate that has been given.

The general properties and composition of the cephalo-rachidian fluid are in brief the following: It is transparent and colorless, free from viscidity, of a distinctly saline taste, an alkaline reaction, and it resists putrefaction for a long time. It is not affected by heat or acids. It contains a large proportion of water (981 to 985 parts per thousand), a considerable quantity of sodium chloride, a trace of potassium chloride, sulphates, carbonates and alkaline and earthy phosphates. In addition it contains traces of urea, glucose, sodium lactate, fatty matter, cholesterine and albumen.

As a summary of the office of the cephalo-rachidian fluid, it may be stated in general terms that it serves to protect the cerebro-spinal axis, chiefly by equalization of the pressure in the varying condition of the blood-vessels, filling the space between the centres and the bony cavities in which they are contained. That the blood-vessels of the cerebro-spinal axis are subject to variations in tension, is readily shown by introducing a canula into the subarachnoid space, when the jet of fluid discharged will be increased with every violent muscular effort. The pressure of the fluid, in this instance, could be affected only through the blood-vessels.

## Physiological Anatomy of the Spinal Cord.

The spinal cord, with its membranes, the roots of the spinal nerves and the surrounding liquid, occupies the spinal canal and is continuous with the encephalon. Its length is fifteen to eighteen inches (38·1 to 45·7 centimetres) and its weight is about an ounce and a half (42·5 grammes). Its general form is cylindrical, but it is slightly flattened in certain portions. It extends from the foramen magnum to the lower border of the body of the first lumbar vertebra. It presents, at the origin of the brachial nerves, an elongated ovoid enlargement flattened antero posteriorly, and a corresponding enlargement at the origin of the nerves which supply the lower extremities. It terminates below in a slender, gray filament, called the filum terminale. The sacral and coccygeal nerves, after their origin from the lower portion of the cord, pass downward to emerge by the sacral foramina, and they form what is known as the cauda equina. The substance of the cord is composed of white and gray matter, the white matter being external. The inferior, pointed termination of the cord consists entirely of gray matter.

The cord is marked by an anterior and a posterior median fissure, and by imperfect and somewhat indistinct anterior and posterior lateral grooves,

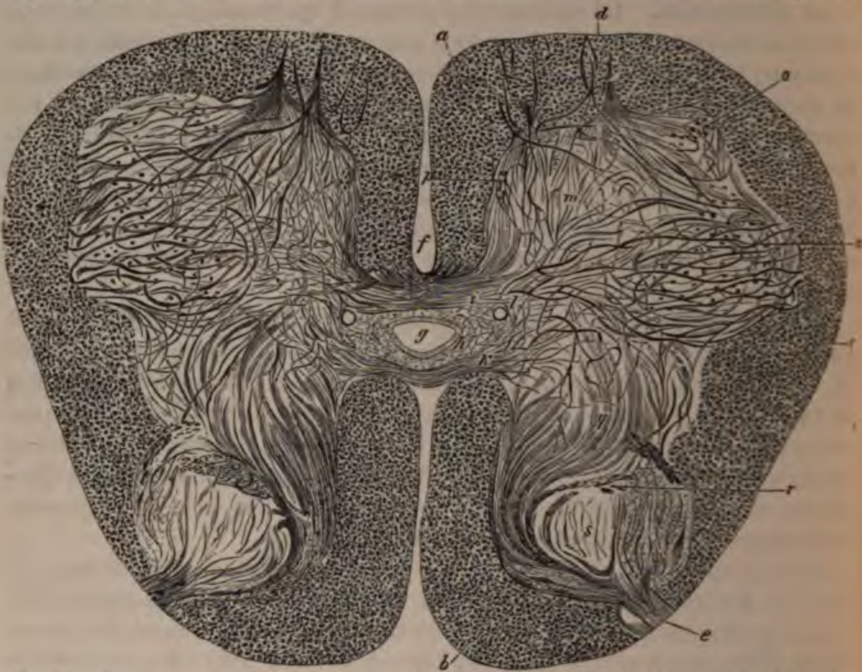


FIG. 216.—*Transverse section of the spinal cord of a child six months old, at the middle of the lumbar enlargement, treated with potassium-auric chloride and uranium nitrate; magnified 20 diameters. By means of these reagents, the direction of the fibres in the gray substance is rendered unusually distinct* (Gerlach).

*a*, anterior columns; *b*, posterior columns; *c*, lateral columns; *d*, anterior roots; *e*, posterior roots; *f*, anterior white commissure, in communication with the fasciculi of the anterior cornua and the anterior columns; *g*, central canal with its epithelium; *h*, surrounding connective substance of the central canal; *i*, transverse fasciculi of the gray commissure in front of the central canal; *k*, transverse fasciculi of the gray commissure behind the central canal; *l*, transverse section of the two central veins; *m*, anterior cornua; *n*, great, lateral cellular layer of the anterior cornua; *o*, lesser, anterior cellular layer; *p*, smallest, median cellular layer; *q*, posterior cornua; *r*, ascending fasciculi in the posterior cornua; *s*, substantia gelatinosa.

from which latter arise the anterior and the posterior roots of the spinal nerves. The posterior lateral groove is tolerably well marked, but there is no distinct line at the origin of the anterior roots. The anterior median fissure is perfectly distinct. It penetrates the anterior portion of the cord, in the median line, for about one-third of its thickness and receives a highly vascular fold of the pia mater. It extends to the anterior white commissure. The posterior fissure is not so distinct as the anterior, and it is not lined throughout by a fold of the pia mater, but is filled with connective tissue and blood-vessels, which form a septum posteriorly, between the lateral halves of the cord. The posterior median fissure extends nearly to the centre of the cord, as far as the posterior gray commissure.

The arrangement of the white and the gray matter in the cord is seen in a transverse section. The gray substance is in the form of a letter H, presenting two anterior and two posterior cornua connected by what is called the gray commissure. The anterior cornua are short and broad, and they do not reach to the surface of the cord. The posterior cornua are larger and narrower, and they extend nearly to the surface, at the point of origin of the posterior roots of the spinal nerves. In the centre of the gray commissure, is a narrow canal, lined by cells of ciliated epithelium, called the central canal. This is in communication above with the fourth ventricle, and it extends below to the filum terminale. That portion of the gray commissure situated in front of this canal is sometimes called the anterior gray commissure, the posterior portion being known as the posterior gray commissure. The central canal is immediately surrounded by connective tissue. In front of the gray commissure, is the anterior white commissure.

The proportion of the white to the gray substance is variable in different portions of the cord. In the cervical region, the white substance is most abundant, and in fact it progressively increases in quantity from below upward throughout the whole extent of the cord. In the dorsal region, the gray matter is least abundant, and it exists in greatest quantity in the lumbar enlargement.

The white substance of the cord is composed of nerve-fibres, connective-tissue elements (neuroglia) and blood-vessels, the latter arranged in a very wide and delicate plexus. The nerve-fibres are variable in size and are composed of the axis-cylinder and the medullary substance, without the tubular membrane.

The anterior cornua of gray matter contain blood-vessels, connective-tissue elements (neuroglia), very fine nerve-fibres, and large multipolar nerve-cells, which are sometimes called motor cells. The posterior cornua are composed of the same elements, the cells being much smaller, and the fibres exceedingly small, presenting very fine plexuses. The cells in this situation are sometimes called sensory cells. Near the posterior portion of each posterior cornu, is an enlargement, of a gelatiniform appearance, containing small cells and fibres, called the substantia gelatinosa. The connections between the nerve-cells and the nerve-fibres have already been described in connection with the general structure of the nervous system. The multipolar nerve-cells are supposed to present certain prolongations which do not branch and are directly connected with the medullated nerve-fibres. These are called axis-cylinder prolongations. In addition, fine, branching poles are described under the name of protoplasmic prolongations. In both the white and the gray substance of the cord, is a ground-work of delicate connective-tissue fibres and cells, called neuroglia. This supports the nerve-cells, nerve-fibres, vessels etc. The neuroglia is particularly abundant in that part of the posterior cornua of gray matter, called the substantia gelatinosa.

The division of the spinal cord into columns has a physiological as well as an anatomical basis. Anatomists usually recognize, on either side of the cord, an anterior column, bounded by the anterior median fissure and the line of origin of the anterior roots of the spinal nerves, a lateral column, bounded by the lines of origin of the anterior and of the posterior roots of the nerves, and a posterior column, bounded by the line of the posterior roots of the spinal nerves and the posterior median fissure. As the anterior or posterior columns include either the white or the gray matter, they are called respectively the anterior or posterior white and gray columns. Physiological and pathological researches, however, have shown that the cord may properly be farther divided as follows :

1. *Columns of Türck.*—By the sides of the anterior median fissure, are two narrow columns of white matter, one on either side, extending to the white commissure (A, in Fig. 217), called the columns of Türck, the direct, or the uncrossed pyramidal tracts. The fibres of these columns descend, probably decussate in the cervical region of the cord, and the columns are lost in the lower dorsal region. Destruction of certain motor parts in the brain is followed by descending secondary degeneration of the fibres of these columns.

2. *Crossed Pyramidal Tracts.*—These are situated, one on either side, in the posterior portion of the lateral columns (G, G, in Fig. 217), and are bounded internally by the posterior cornua of gray matter and externally by a narrow band called the direct cerebellar tract. In following the columns upward, it is found that they pass forward in the upper part of the cervical region and decussate in the lower portion of the anterior pyramids of the medulla oblongata. These are descending tracts, and their fibres undergo descending secondary degeneration as the result of destruction of certain motor parts in the brain.

3. *Anterior Fundamental Fasciculi.*—These fasciculi (B, in Fig. 217), are bounded internally by the columns of Türck and externally by the anterior cornua of gray matter and the anterior roots of the spinal nerves. Their fibres are supposed to connect the gray matter of the anterior cornua of the cord with the gray matter of the medulla oblongata.

4. *Anterior Radicular Zones.*—These columns (E, E, in Fig. 217) are in the anterior portion of the lateral columns. Their fibres are supposed to connect the gray matter of the cord with the gray matter of the medulla oblongata.

5. *Mixed Lateral Columns.*—These columns (F, F, in Fig. 217) are in the lateral columns of the cord, next the gray matter. With the anterior fundamental fasciculi and the anterior radicular zones, they probably connect the gray matter of the cord with the gray matter of the medulla oblongata.

The fibres of the anterior fundamental fasciculi, the anterior radicular zones and the mixed lateral columns do not degenerate in either direction as the result of section of the cord. Their fibres seem to connect nerve-cells with each other, and their trophic cells exist at both extremities, which accounts for the absence of degeneration, just mentioned.

6. *Direct Cerebellar Fasciculi.*—These fasciculi (H, H, in Fig. 217) are situated at the outer and posterior portion of the lateral columns. Their fibres pass to the funiculi graciles, or posterior pyramids of the medulla oblongata, and thence to the cerebellum, by the inferior peduncles. They connect the cells of the posterior cornua of gray matter with the cerebellum. These columns make their appearance first in the lumbar region of the cord, and they increase in size from below upward. After section of the spinal

cord, the fibres of the direct cerebellar fasciculi show ascending secondary degeneration. Their trophic centres probably are the cells of the posterior cornua of gray matter of the cord.

7. *Columns of Burdach.*—These columns (D, in Fig. 217) are in the posterior columns of the cord, between the columns of Goll and the posterior cornua of gray matter. Their fibres connect some of the cells of the gray matter of the posterior cornua with the cerebellum; or at least the fibres pass upward and are connected with the restiform bodies, going to the cerebellum through the inferior peduncles. The fibres also connect nerve-cells of different portions of the cord with each other. No secondary degenerations have been noted in these columns.

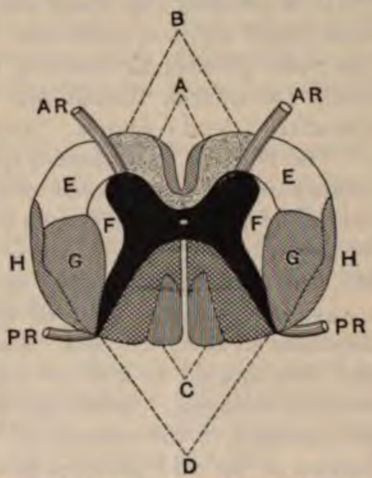


FIG. 217.—*Diagram of the columns and conducting paths in the spinal cord in the upper dorsal region* (enlarged and modified from Landois).

AR, AR, anterior roots of the spinal nerves; PR, PR, posterior roots; A, columns of Türck; B, anterior fundamental fasciculi; C, columns of Goll; D, columns of Burdach; E, E, anterior radicular zones; F, F, mixed lateral columns; G, G, crossed pyramidal tracts; H, H, direct cerebellar fasciculi. The gray matter of the cord is in black. The figure also shows the anterior and posterior median fissures, the white and gray commissures and the central canal.

8. *Columns of Goll*—These delicate columns (C, in Fig. 217) are situated on either side of the posterior median fissure. They are lost in the lower dorsal or upper lumbar region. Their fibres pass upward and are lost in the funiculi graciles of the medulla oblongata. After section of the cord, ascending secondary degeneration is observed in the fibres of these columns.

*Directions of Nerve-Fibres in the Cord.*—Many of the points in the description of the course and connections of the fibres in the cord are given as probable. Anatomical observations have been somewhat contradictory, but these have been corrected or verified by following the paths of degeneration. What is called secondary degeneration is the anatomical change in the nerve-fibres which follows separation of the fibres from the cells which act as their trophic centres, or the centres presiding over their nutrition, these changes being secondary to the destruction or degeneration of the centres.

The fibres of the anterior roots of the spinal nerves, following these fibres inward and upward, pass directly to the large, multipolar motor cells of the anterior cornua of gray matter and have no direct connection with the white columns. Their direction through the white columns of the cord is oblique and slightly upward. They are continuous with the axis-cylinder prolongations of the cells. From the nerve-cells, prolongations are given off, by branching processes, in two bundles, median and lateral. The fibres of the median bundle pass to the anterior white commissure, in which they decussate. They then go each one to the column of Türck on the opposite side and pass upward in the so-called direct pyramidal tracts. The fibres of the lateral bundle go to the crossed pyramidal tract in the lateral column of the same side and pass upward to decussate at the medulla oblongata.

The fibres of the columns of Türck and the crossed pyramidal tracts are the only fibres of the cord which are known to convey motor impulses from the brain. Destruction of certain parts of the brain produces descending secondary degeneration of these fibres.

It is probable that fibres arise from the cells of the gray matter of the cord, which connect these cells with each other and are concerned in certain reflex phenomena involving the action of the cord alone. These fibres are in the anterior fundamental fasciculi, the anterior radicular zones and the mixed lateral columns. They present no secondary degeneration.

The fibres of the posterior roots of the spinal nerves pass to the small, sensory cells of the posterior cornua of gray matter of the cord and are connected by branching processes with branching prolongations of these cells. Processes from these cells pass to the gray commissure and decussate around the central canal, conducting sensory impressions to the brain, in the gray matter of the opposite side of the cord. The sensory conductors therefore decussate all along the cord. Some of the fibres go to the columns of Goll and pass upward to and are continuous with the funiculi graciles of the medulla oblongata. Fibres also pass to the direct cerebellar fasciculi and a few, perhaps, to the columns of Burdach, to go upward to the cerebellum. Section of the cord produces ascending secondary degenerations in the columns of Goll and the direct cerebellar fasciculi. Fibres originating in the nerve-cells of the posterior cornua pass in and out, along the cord, and connect the cells with each other. These may properly be called longitudinal commissural fibres. They probably constitute the greater part of the columns of Burdach and they present no secondary degeneration.

## General Properties of the Spinal Cord.

As regards the general properties of the cord, as shown by the effects of stimulus applied to its exterior or to its cut surface, the term excitability will be used to express a property indicated by direct muscular contraction following stimulation of the cord, and sensibility, a property which enables it to receive impressions which produce pain. In exciting different parts of the cord with electricity, it is necessary to carefully guard against an extension of the current beyond the points which it is intended to stimulate. Some physiologists regard the cord as absolutely inexcitable and insensible, both on its surface and in its deeper portions. With this view, it is supposed that parts of the cord will conduct motor impulses received from the centres situated above, but are not excited by a stimulus applied directly. In the same way, it is thought, parts of the cord will convey sensory impressions received through the nerves, but are insensible to direct irritation.

The results of the observations of Van Deen, Brown-Séquard, Schiff and others, were simply negative; but the positive results obtained by Longet, Fick, Vulpian and those who regard parts of the cord as excitable and sensible, show that certain of the columns react under direct stimulation.

In some experiments made in 1863 (Flint) upon a living dog, the cord having been exposed in the lumbar region and stimulated mechanically and with an electric current two hours after the operation, certain positive results were obtained, which led to the following conclusions:

The gray substance is probably inexcitable and insensible under direct stimulation.

The antero-lateral columns are insensible, but are excitable both on the surface and in their substance; and direct stimulation of these columns produces convulsive movements in certain muscles, which movements are not reflex and are not attended with pain. The lateral columns are less excitable than the anterior columns.

The surface, at least, of the posterior columns is very sensitive, especially near the posterior roots of the nerves. The deep portions of the posterior columns are probably insensible, except very near the origin of the nerves.

The above conclusions refer only to the general properties of different portions of the cord, as shown by direct stimulation, in the same way that the general properties of the nerves in their course are demonstrated.

*Motor Paths in the Cord.*—What has been said regarding the direction of the fibres in the cord and the situation and course of the degenerations following destruction of motor cerebral centres conveys a definite idea of the motor paths in the cord. This idea is sustained by experiments in which different columns of the cord have been divided in living animals.

The motor paths are in the direct pyramidal tracts (columns of Türck) and in the crossed pyramidal tracts of the lateral columns. The motor impulses are conveyed by the fibres of these tracts to the multipolar cells in the anterior cornua of gray matter and are thence transmitted to the anterior roots of certain spinal nerves. In the lower dorsal region the conduction is confined to the crossed pyramidal tracts in the lateral columns, while above, the direct pyramidal tracts participate in this action.

The motor fibres decussate in the anterior pyramids of the medulla oblongata (crossed pyramidal tracts), and in the cervical region, to a comparatively slight extent, before the direct pyramidal tracts (columns of Türck) pass to the encephalon. In the cervical region the decussation takes place probably in the anterior white commissure. The fact of this decussation of motor conductors is sustained by pathology—paralysis of motion following brain-lesions, occurring on the opposite side of the body—and by experiments in which the fibres as they cross are divided by a longitudinal median section in the medulla and in the cervical region of the cord.

Vaso-motor nerve-fibres exist in the lateral columns of the cord and probably are connected with the cells of the gray matter. They pass out in the anterior roots of the spinal nerves and go to the blood-vessels either from the branches of the spinal nerves directly or through filaments sent to the sympathetic.

*Sensory Paths in the Cord.*—The gray matter of the cord is the part concerned in the conduction of sensory impressions (Bellingeri, 1823). This fact has been verified by recent experiments; but it is thought that some of the sensory conductors run in the columns of Goll (Flechsig). The columns of Goll, however, exist only in the cervical and dorsal regions.

The sensory conductors do not decussate at any particular point as do the motor conductors in the crossed pyramidal tracts. The fibres from the posterior roots of the spinal nerves pass to the sensory cells of the posterior cornua and decussate throughout the entire length of the cord (Brown-Séquard). If the cord be divided longitudinally in the median line, there is complete paralysis of sensation on both sides in all parts below the section (Fodéra, 1822, and Brown-Séquard). In this section, the only fibres that are divided are those passing from one side of the cord to the other. This decussation is by fibres prolonged from the cells of the posterior cornua, which cross in the gray commissure, around the central canal.

When one lateral half of the cord is divided in a living animal, sensibility is impaired or lost on the opposite side of the body, below the section, but there is hyperæsthesia on the side corresponding to the section. The exaggeration of sensibility has not been satisfactorily explained.

*Relations of the Posterior White Columns of the Cord to Muscular Co-ordination.*—It was noticed by Todd, many years ago (1839–1847), in cases of that peculiar form of muscular inco-ordination now known as locomotor ataxia, that the posterior white columns of the cord were diseased. Reasoning from this fact, Todd made the following statement with regard to the office of these columns:

"I have long been impressed with the opinion, that the office of the posterior columns of the spinal cord is very different from any yet assigned to them. They may be in part commissural between the several segments of the cord, serving to unite them and harmonize them in their various actions, and in part subservient to the function of the cerebellum in regulating and co-ordinating the movements necessary for perfect locomotion."

The view thus early advanced by Todd has been sustained by the results of experiments on living animals. If the posterior columns be completely divided, by two or three sections made at intervals of about three-fourths of an inch to an inch and a quarter (20 to 30 mm.), the most prominent effect is a remarkable trouble in locomotion, consisting in a want of proper co-ordination of movements (Vulpian). Experiments upon the different columns of the cord in living animals, however, are so difficult that physiologists have preferred to take the observations in cases of disease in the human subject as the basis of their ideas with regard to the office of the posterior white columns.

The characteristic phenomenon of locomotor ataxia is inability to co-ordinate muscular movements, particularly those of the extremities. There is not of necessity any impairment of actual muscular power; and although pain and more or less disturbance of sensibility are usual, these conditions are not absolutely invariable and they are always coincident with disease of sensory conductors. The characteristic pathological condition is disease of the posterior white columns (columns of Burdach). This is usually followed by or is co-existent with disease of the posterior roots of the spinal nerves and disease of the cells of the posterior gray matter of the cord. As the cells are affected, there follows ascending secondary degeneration of the columns of Goll. It is fair to assume that the disease of the cells of the gray matter of the cord and of the posterior roots of the spinal nerves is connected with the disorders of general sensibility. The disease of the columns of Burdach produces the disorder in movements.

Reasoning from the characteristic phenomena and the essential pathological conditions of the cord in typical cases of locomotor ataxia, the posterior white columns of the cord, connecting cells of the gray matter in different planes with each other, assist in regulating and co-ordinating the voluntary movements. The fibres of these columns also connect the cord with the cerebellum, which has an important office in muscular co-ordination. It is probable that the appreciation of the muscular sense and the sense of pressure, if these can be separated from what is known as general sensibility, are connected with the action of the fibres of the posterior white columns.

## Nerve-Centres in the Spinal Cord.

It has long been known that decapitation of animals does not arrest muscular action; and the movements observed after this mutilation present a certain degree of regularity and have been shown to be in accordance with well defined laws. Under these conditions, the regulation of such movements is effected through the spinal cord and the spinal nerves. If an animal be decapitated, leaving only the cord and its nerves, there is no sensation, for the parts capable of appreciating sensation are absent; nor are there any true voluntary movements, as the organ of the will is destroyed. Still, in decapitated animals, the sensory nerves are for a time capable of conducting impressions, and the motor nerves can transmit a stimulus to the muscles; but the only part capable of receiving an impression or of generating a motor impulse is the gray matter of the cord. If in addition to the removal of all of the encephalic ganglia, the cord itself be destroyed, all muscular movements are abolished, except as they may be produced by direct stimulation of the muscular tissue or of individual motor nerves.

The gray matter of the brain and spinal cord is a connected chain of ganglia, capable of receiving impressions through the sensory nerves and of generating motor impulses. The cerebro-spinal axis, taken as a whole, has this general office; but some parts have separate and distinct properties and can act independently of the others. The cord, acting as a conductor, connects the brain with the parts to which the spinal nerves are distributed. If the cord be separated from the brain in a living animal, it may act as a centre, independently of the brain; but the encephalon has no communication with the parts supplied with nerves from the cord, and it can act only upon the parts which receive nerves from the brain itself.

When the cord is separated from the encephalon, an impression made upon the general sensory nerves is conveyed to its gray substance, and this gives rise to a stimulus, which is transmitted to the voluntary muscles, producing certain movements, independently of sensation and volition. This impression is said to be reflected back from the cord through the motor nerves; and the movements occurring under these conditions are called reflex. As they are movements excited by stimulation of sensory nerves, they are sometimes called excito-motor.

The term reflex, as it is now generally understood by physiologists, may properly be applied to any generation of nerve-force which occurs as a consequence of an impression received by a nerve-centre; and it is evident that reflex phenomena are by no means confined to the action of the spinal cord. The movements of the iris are reflex, and yet they take place in many instances without the intervention of the cord. Movements of the intestines and of the involuntary muscles generally are reflex, and they involve the action of the sympathetic system of nerves. Impressions made upon the nerves of special sense, as those of smell, sight, hearing etc., give rise to certain trains of thought. These involve the action of the brain, but still they are reflex. In this last example of reflex action, it is sometimes difficult to connect the operations of the mind with external impressions as an exciting cause; but it is evident, from a little reflection, that this is often the case.

*Reflex Action of the Spinal Cord.*—Simple reflex action involves the existence of an afferent (sensory) nerve, a collection of nerve-cells, and an efferent (motor) nerve, the nerves being connected with the nerve-cells. In a decapitated animal, not only are the movements independent of sensation and volition, but no movements occur if the sensory nerves be protected from any kind of impression or stimulation (Marshall Hall, 1832 and 1833). If the cord be destroyed, however, no movements follow stimulation of the surface; and if either the afferent and the efferent nerves be divided, no reflex movements can take place. Experiments upon decapitated animals are in accord with the results of observations upon acephalous fœtuses and in cases of complete paraplegia from injury to the cord.

In the simplest form of a reflex movement, the muscular contraction is confined to the muscle or muscles which correspond, in their nervous supply, to the afferent nerve stimulated; but when the stimulus is sufficiently powerful or when the cord is in a condition of exalted excitability, the impression is disseminated throughout the gray matter, and the entire muscular system may be thrown into action. With feebler stimulation, one side only of the muscular system may respond. When the reaction extends to the opposite side, it is called crossed reflex. The extension of a stimulus conveyed by a single afferent nerve throughout the cord is called irradiation.

When a feeble stimulus applied to an afferent nerve is repeated frequently and at short intervals, general muscular movements are produced. This follows stimuli applied three times in a second, and the effect is increased up to sixteen shocks in a second, but not beyond this number (Rosenthal).

In studying the paths of conduction in the cord it has been seen that sensory conduction takes place through the gray matter and possibly through the columns of Goll, that motor impulses are conducted by the direct and the crossed pyramidal tracts, and that the columns of Burdach are connected with muscular co-ordination. The fibres of the cord that are specially connected with reflex action are probably in the anterior fundamental fasciculi, the anterior radicular zones and the mixed lateral columns.

It is well known that the reflex excitability of the cord is exaggerated by removal of the encephalon. According to Setschenow (1863), certain parts in the encephalon, particularly the optic lobes in frogs, exert an inhibitory influence over the reflex acts of the cord, and as a consequence, the reflex phenomena are more marked when this influence is suppressed.

Various poisons, especially strychnine, have a remarkable influence over reflex excitability. In a frog decapitated and poisoned with strychnine, no reflex movements occur unless an impression be made on the sensory nerves; but the slightest irritation, such as a breath of air, throws the entire muscular system into a condition of violent tetanic spasm. The same phenomena are observed in cases of poisoning by strychnine or of tetanus in the human subject.

FIG. 218.—*Frog poisoned with strychnine* (Liégeois).

The inhalation of anæsthetic agents may abolish all of the ordinary reflex phenomena. Whether this be due to an action upon the cord itself or to a paralysis of the sensory nerves, it is difficult to determine. Ordinarily, in animals rendered insensible by anæsthetics, the movements of respiration continue; but these also may be arrested, as has been observed by all who have experimented with anæsthetics, especially with chloroform. A common way of determining that an animal is completely under the influence of an anæsthetic is by noting an absence of the reflex act of closing the eyelids when the cornea is touched.

It is only necessary, after what has gone before, to indicate in a general way certain phenomena observed in the human subject which illustrate the reflex action of the cord. It is a common observation, in cases of paraplegia in which the lower portion of the cord is intact, that movements of the limbs follow titillation of the soles of the feet, these movements taking place independently of the consciousness or the will of the subject experimented upon. Acephalous fœtuses will present general reflex movements and movements of respiration, and will even suck when the finger is introduced into the mouth. Observations of this kind are so familiar that they need not be cited in detail. Experiments have also been made upon criminals after decapitation; and although the reflex phenomena are not so well marked and can not be excited so long after death as in cold-blooded animals, they are sufficiently distinct.

General muscular spasms following stimulation of sensory nerves are pathological and take place only when the reflex excitability of the cord is much exaggerated. Examples of this action are the spasms observed in tetanus or in poisoning by strychnine. In experiments on the lower animals, particularly frogs, co-ordinate reflex movements are often observed, such as the movements of jumping or swimming. This is sometimes called purposive reflex action, as the movements seem to have a definite purpose or object. The following well known experiment illustrates a co-ordinate, or purposive reflex:

Pflüger (1853) removed the entire encephalon from a frog, leaving only the spinal cord. He then touched the surface of the thigh, over the inner condyle, with acetic acid. The animal thereupon rubbed the irritated surface with the foot of the same side, apparently appreciating the seat of the irritation, and endeavoring, by a voluntary effort, to remove it. The foot of this side was then amputated, and the irritation was renewed in the same place. The animal made an ineffectual effort to reach the spot with the amputated member, and failing in this, after some general movements of the limbs, rubbed the spot with the foot of the opposite side.

It has been thought that this experiment shows a persistence of sensation and the power of voluntary movements after removal of the entire encephalon; but it must be remembered that the cord contains cells connected together by fibres probably into groups which correspond to sets of muscles concerned in co-ordinate movements, and that many movements set in action by an effort of the will continue in an automatic manner, as the ordinary movements of progression. It is more reasonable to suppose that a persistent stimulation of the surface, such as is produced by the action of acetic acid upon the skin of a frog, can give rise to co-ordinate movements of a purely reflex character than to assume that the movements in Pflüger's experiment are voluntary efforts to remove a painful impression. It is certain that in the higher classes of animals after removal of the encephalon, in experiments on decapitated criminals and in patients suffering from paraplegia, there is no evidence of true sensation or volition in the spinal cord. In man and the higher animals, all muscular movements which depend solely upon the reflex action of the cord must be regarded as automatic and entirely independent of consciousness and of the will.

Certain reflex movements may be restrained by an effort of the will, as is well known; provided, always, that these be movements that can be executed by voluntary effort. Nevertheless, if the sensory impression be sufficiently powerful or be very frequently repeated, it is often impossible to control such movements by the will. Movements that are never in themselves voluntary, such as the ejaculation of semen, when excited by reflex action can not be restrained by a voluntary effort; while the reflex act of coughing, for example, may be measurably controlled. It is hardly proper to speak of inhibition of the reflexes, in the sense in which the term inhibition is generally used in physiology, for the reason that there are probably no special inhibitory nerves for these movements.

Various reflexes are made use of in pathology as means of diagnosis. The superficial reflexes are those produced by tickling the soles of the feet or by exciting other parts of the skin. The most prominent of the deep reflexes is the patellar reflex, or the knee-jerk, produced by percussion of the ligamentum patellæ.

The gray matter of the cord is not a single centre, but consists of a number of centres connected with each other and with the brain. Some of these have already been described in connection with the history of various physiological processes, and others will be considered hereafter under appropriate heads. In addition to those already described, are centres for defecation, at the fifth lumbar vertebra in dogs (Budge), the erection-centre, in the lumbar region (Eckhard), and the parturition-centre (Körner), at the first and second lumbar vertebræ. All of the spinal centres act in accordance with the general laws of reflex phenomena.

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## CHAPTER XIX.

### *THE ENCEPHALIC GANGLIA.*

**Physiological divisions of the encephalon—Weights of the encephalon and of certain of its parts—The cerebral hemispheres—Cerebral Convolutions—Basal ganglia—Corpora striata, optic thalami and internal capsule—Tubercular quadrigemina—Pons Varolii—Directions of the fibres in the cerebrum—Cerebral localization—General uses of the cerebrum—Extirpation of the cerebrum—Facial angle—Pathological observations—Reaction-time—Centre for the expression of ideas in language—The cerebellum—Physiological anatomy—Extirpation of the cerebellum—Pathological observations—Connection of the cerebellum with the generative function—Medulla oblongata (Bulb)—Physiological anatomy—Uses of the medulla oblongata—Respiratory nerve-centre—Cardiac centres—Vital point (so called)—Rolling and turning movements following injury of certain parts of the encephalon.**

THE encephalic ganglia are collections of gray matter found in the encephalon, or what is commonly known as the brain. This part of the cerebro-spinal axis is situated in the cranial cavity. It is provided with membranes, which are similar to the membranes of the spinal cord and have been described in connection with the cord and the general arrangement of the cerebro-spinal axis. The gross anatomical divisions of the encephalon are the cerebrum, cerebellum, pons Varolii and medulla oblongata. As regards their physiological uses, the cerebellum, pons and medulla are to a certain extent subordinate to the cerebrum. In treating of the physiology of these parts, it will be convenient to take up first the cerebrum, or the cerebral hemispheres, with their anatomical and physiological connections and their relations to the other parts of the encephalon.

All parts of the encephalon which act as nerve-centres are more or less intimately connected with each other anatomically, and are finally connected, through the medulla oblongata, with the spinal cord. The exceptions to this rule are the centres of olfaction, vision, audition and gustation, which will be considered fully in connection with the physiology of the special senses. The spinal cord, as has been seen, is capable of independent action as a nerve-centre or collection of nerve-centres, also serving as a means of connection between the brain and the parts, through the spinal nerves. The motor and sensory cranial nerves are directly connected with the encephalon.

A detailed anatomical description of the brain would be out of place in this work, as there are many anatomical parts, the exact physiological relations of which are not understood; still, there are certain parts which will be referred to by name, a general knowledge of the arrangement of which is necessary. The general relations of these parts are shown in Fig. 219, slightly reduced and modified, from Harrison Allen, which represents a vertical longitudinal section of the brain, in the median line.

As bearing upon certain points in the physiology of the brain, it is important to note the weight of the entire encephalon and of its great divisions.

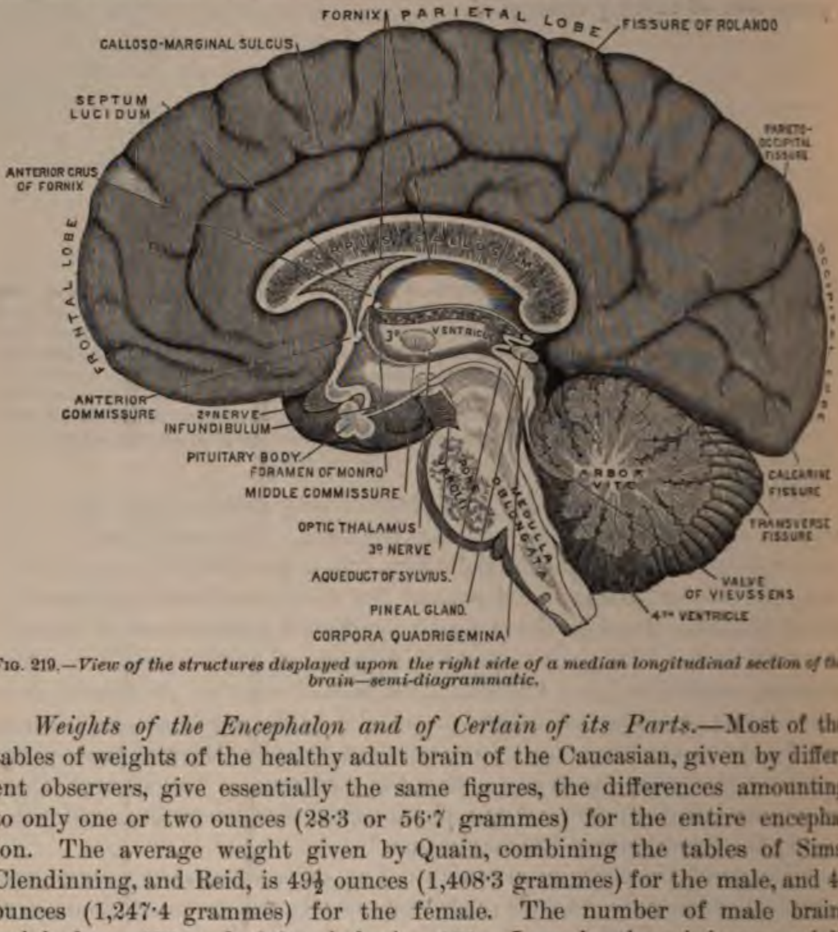



FIG. 219.—*View of the structures displayed upon the right side of a median longitudinal section of the brain—semi-diagrammatic.*

*Weights of the Encephalon and of Certain of its Parts.*—Most of the tables of weights of the healthy adult brain of the Caucasian, given by different observers, give essentially the same figures, the differences amounting to only one or two ounces (28·3 or 56·7 grammes) for the entire encephalon. The average weight given by Quain, combining the tables of Sims, Clendinning, and Reid, is 49½ ounces (1,408·3 grammes) for the male, and 44 ounces (1,247·4 grammes) for the female. The number of male brains weighed was 278, and of female brains, 191. In males the minimum weight was 34 ounces (963·9 grammes), and the maximum, 65 ounces (1,842·7 grammes). In 170 cases out of the 278, the weights ranged between 46 and 53 ounces (1,304·1 and 1,502·5 grammes), which may be taken as the average limits. In females the minimum was 31 ounces (878·8 grammes), and the maximum, 56 ounces (1,587·6 grammes). In 125 cases out of the 191, the weights ranged between 41 and 47 ounces (1,162·3 and 1,332·4 grammes).

Quain assumed, from various researches, that in new-born infants, the brain weighs 11·65 ounces (327·8 grammes), for the male, and 10 ounces (283·5 grammes), for the female. In both sexes, "the weight of the brain generally increases rapidly up to the seventh year, then more slowly to between sixteen and twenty, and again more slowly to between thirty-one and forty, at which time it reaches its maximum point. Beyond that period, there appears a slow but progressive diminution in weight of about one ounce (28·3 grammes) during each subsequent decennial period; thus confirming the opinion, that the brain diminishes in advanced life."

The comparative weights of the several parts of the encephalon, calculated by Reid from observations upon the brains of fifty-three males and thirty-four females between the ages of twenty-five and fifty-five, are as follows:

| Divisions of the encephalon. | Males. | Females. |
|---|---|---|
| Average weight of the cerebrum | 43·98 oz. (1,247·3 grammes). | 38·75 oz. (1,098·6 grammes). |
| Average weight of the cerebellum.................... | 5·25 " (148·8 grammes). | 4·76 " (134·9 grammes). |
| Average weight of the pons and medulla oblongata.......... | 0·98 " (28·2 grammes). | 1·01 " (28·6 grammes). |
| Average weight of the entire encephalon......... | 50·21 oz. (1,423·5 grammes). | 44·52 oz. (1,262·1 grammes). |

The proportionate weight of the cerebellum to that of the cerebrum, in the male, is as 1 to 8$\frac{4}{7}$, and in the female, as 1 to 8$\frac{1}{4}$ (Quain).

The specific gravity of the whole encephalon is about 1036, that of the gray matter being 1034, and of the white, 1040 (Quain).

## THE CEREBRAL HEMISPHERES.

*Cortical Substance.*—The surface of the cerebral hemispheres is marked by fissures and convolutions, which serve to increase the extent of the gray substance. The sulci between the convolutions vary in depth in different parts, the average depth being about an inch (25·4 mm.). The gray matter, which is external and follows the convolutions, is $\frac{1}{12}$ to $\frac{1}{8}$ of an inch (2·1 to 3·2 mm.) in thickness. Anatomists have described this substance as existing in several layers, but this division is mainly artificial. In certain parts, however, particularly in the posterior portion of the cerebrum, the gray substance is quite distinctly divided into two layers, by a very delicate, intermediate layer of a whitish color.

There is a marked difference in the appearance of the cells in the most superficial and in the deepest portions of the gray substance. The superficial cells are small and present a net-work of delicate, anastomosing fibres. The deepest cells are much larger. Between these two extremes, in the intermediate layers, there is a gradual transition in the size of the cells. Fig. 220 shows the layers of cells in a vertical section of a cerebral convolution. The most superficial layer is very thin. It contains much neuroglia and a fine net-work of fibrils, with a few small nerve-cells. The second layer presents a large number of small, so-called pyramidal cells. The third layer


FIG. 220.—*Vertical section of the third cerebral convolution in man* (Meynert).

1, superficial layer; 2, layer of small pyramidal cells; 3, layer of large pyramidal cells; 4, layer of small irregular cells; 5, layer of spindle-shaped cells; M, white substance.

is the thickest of all and contains large, pyramidal cells, which become larger in its deeper portions. The fourth layer contains a large number of smaller cells, irregular in form and with branching prolongations. The fifth layer presents spindle-shaped cells with branching poles and this layer is just above the white substance. The pyramidal cells present a long process above, which passes toward the surface, lateral branches, which form a plexus of fine fibrils, and an unbranched prolongation below, which passes to the white substance, in the form of an axis-cylinder. The cells vary somewhat in their appearances in different parts of the brain. The largest pyramidal cells are found in the anterior central convolution, in the upper part of the posterior central convolution and the paracentral lobule. Large cells with few prolongations are found in the posterior part of the occipital lobes. The cells in this part are connected together by communicating poles. The mode of connection of the cells with each other and with the fibres of the white substance has already been described and does not demand farther mention.

*Cerebral Convolutions.*—The cerebrum presents a great longitudinal median fissure by which it is partially divided into two lateral halves. Fig. 221, which is based on the well known diagram of the brain, by Ecker, shows three great fissures, the fissure of Sylvius, the fissure of Rolando and the parieto-occipital fissure. The lobes of the cerebrum are (1) the frontal lobe, lying in front of and above the fissure of Sylvius and in front of the fissure of Rolando, (2) the parietal lobe, behind the frontal lobe and in front of ıd above the occipital lobe, (3) the occipital lobe, and (4) the temporo-ıhenoidal lobe. The parietal lobe is bounded in front by the fissure of

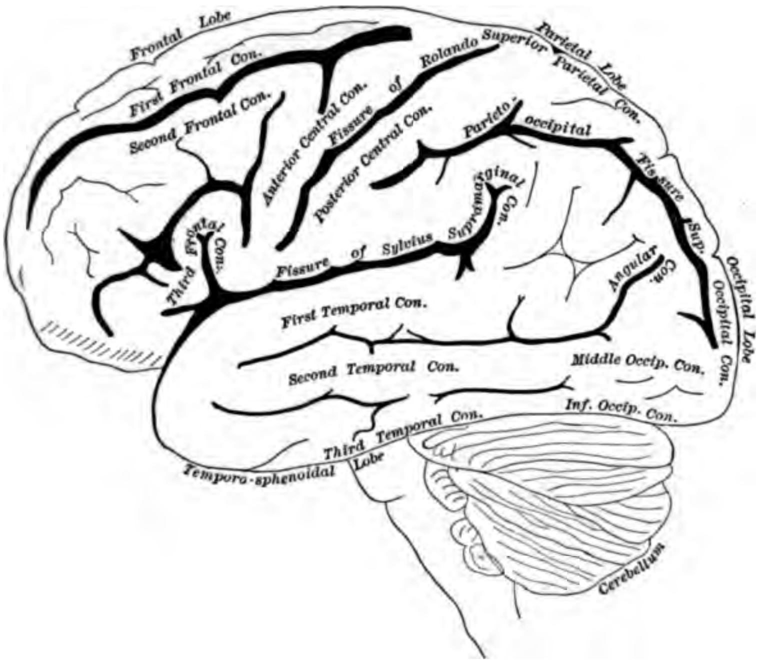
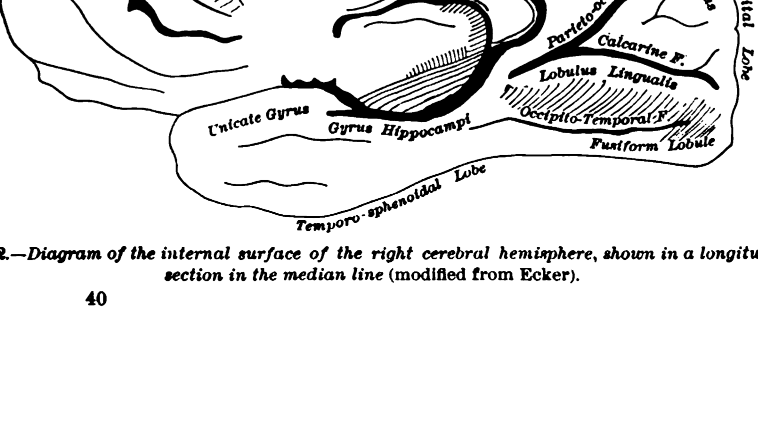



**FIG. 221.**—*Diagram of the external surface of the left cerebral hemisphere* (modified from Ecker).

ɔlando and below by the fissure of Sylvius and the parieto-occipital fissure hown in Fig. 222). The occipital lobe lies below the parieto-occipital fis-




ı. **222.**—*Diagram of the internal surface of the right cerebral hemisphere, shown in a longitudinal section in the median line* (modified from Ecker).

sure. The temporo-sphenoidal lobe is situated below the fissure of Sylvius and in front of the occipital lobe.

While the convolutions are not exactly the same in all human brains, or even in both sides of the brain, their arrangement and relations may be described in a general way with sufficient accuracy to enable one to recognize easily the most important physiological points in the descriptive anatomy of the cerebral surface. The diagrammatic Figs. 221 and 222 give a general view of the fissures and of the most important convolutions.

The first frontal convolution is bounded internally by the great longitudinal fissure and externally by a shallow fissure nearly parallel to the longitudinal fissure. The second frontal convolution lies next the first frontal convolution, and is bounded externally by two shallow fissures lying in front of the fissure of Sylvius. The third frontal convolution curves around the short branch of the fissure of Sylvius. On either side of the fissure of Rolando, are the anterior central convolution and the posterior central convolution. Curving around the posterior extremity of the fissure of Sylvius, is the supramarginal convolution, which is continuous with the first temporal convolution, the latter lying behind and parallel with the fissure of Sylvius. Internal to the posterior portion of the parieto-occipital fissure, is the angular convolution, which is continuous with the second temporal convolution. At the inferior border of the temporo-sphenoidal lobe, below the first and second temporal convolutions, is the third temporal convolution. The superior parietal convolution lies by the side of the median fissure and is the posterior continuation of the first frontal convolution. The situation of the occipital convolutions is indicated in Fig. 221. In addition to these convolutions upon the general surface of the cerebrum, there are convolutions on the surface of the base of the brain and in the gray matter of the sides of the great longitudinal fissure. In the fissure of Sylvius, near its ascending branch, between the anterior and the posterior lobes of the brain and beneath the third frontal convolution, is a group of convolutions constituting the island of Reil.

Fig. 222 shows the most important parts observed on the inner surface of the right hemisphere. These parts do not demand any explanation beyond that given in the diagram itself.

*Basal Ganglia.*—The ganglia at the base of the brain are the olfactory ganglia, the corpora striata, optic thalami, tubercula quadrigemina and the gray matter of the pons varolii. The olfactory ganglia will be described in connection with the physiology of the sense of smell. The corpora striata and the optic thalami are important in their relations to the internal capsule and the paths of motor and sensory conduction.

*Corpora Striata, Optic Thalami and Internal Capsule.*—The corpora striata are pear-shaped bodies, situated at the base of the brain, with their rounded bases directed forward, and the narrower ends, backward and outward. Their external surface is gray, and they present, on section, alternate striæ of white and gray matter. Between the posterior and narrow extremities of these bodies, are the optic thalami. The corpora striata have what is called an intraventricular portion, projecting into the anterior part of the lateral ventricles, and an extraventricular portion, which is embedded in the white substance at the base of the brain.

The optic thalami are oblong bodies situated between the posterior extremities of the corpora striata and resting upon the crura cerebri on the two sides. These are white externally, and in their interior they present a mixture of white and gray matter.

If a horizontal section be made through the brain, involving the corpora striata and the optic thalami, the corpora striata present a division into two nuclei. These are the caudate nucleus, which is internal, and the lenticular nucleus, which is external to and behind the caudate nucleus. External to the lenticular nucleus, is a band of white substance, called the external capsule, in which there is a band of gray matter, called the claustrum. External to the external capsule, at its anterior portion, is the insula, or island of Reil.

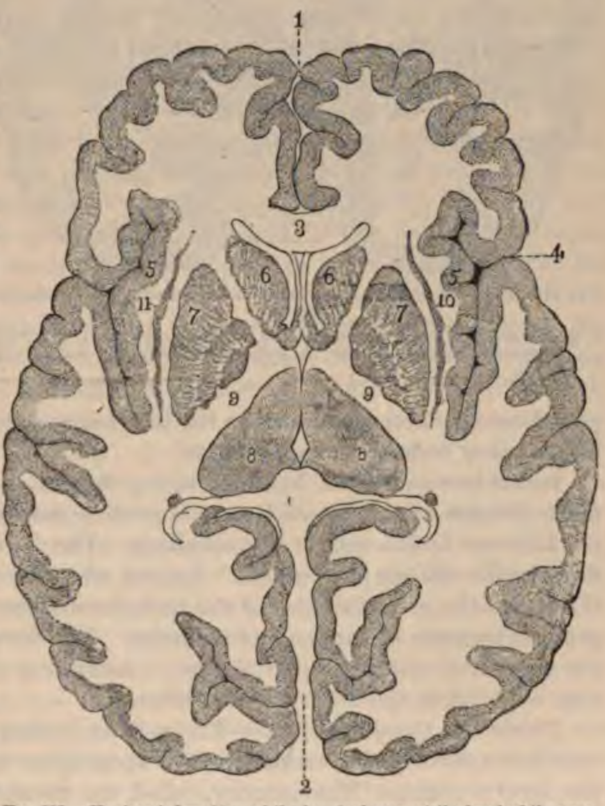



FIG. 223.—*Horizontal section of the hemispheres, at the level of the cerebral ganglia* (Dalton).

1, great longitudinal fissure between the frontal lobes; 2, great longitudinal fissure between the occipital lobes; 3, anterior part of the corpus callosum; 4, fissure of Sylvius; 5, convolutions of the insula; 6, caudate nucleus of the corpus striatum; 7, lenticular nucleus of the corpus striatum; 8. optic thalamus; 9, internal capsule; 10, external capsule; 11, claustrum.

Between the caudate nucleus and the lenticular nucleus in front, is a broad band of white fibres, which is continuous with a band of white fibres lying posteriorly, between the lenticular nucleus and the optic thalamus on either side. This band is the internal capsule. The portion of the internal capsule which lies between the caudate nucleus and the lenticular nucleus is called its anterior division. The portion of the internal capsule situated between the lenticular nucleus and the optic thalamus is its posterior division. The bend where the posterior division of the internal capsule joins the anterior division is called the knee of the capsule.

The directions of the fibres of the internal capsule are in general terms the following: Fibres from the crura cerebri go directly into the corpora striata in front and into the optic thalami behind. This is the course of the greater part of the fibres, but some fibres go directly through the internal capsule, and thence to the gray matter of the cerebral convolutions. Most of the fibres, however, which form the internal capsule, come from the gray matter of the corpora striata and optic thalami and curve outward and upward to go to the gray matter of the hemispheres. As they pass from the internal capsule to the internal surface of the cerebral convolutions, they form the corona radiata.


FIG. 224.—*Diagram of the human brain in a transverse vertical section* (Dalton).

1, pons Varolii; 2, 2, crura cerebri; 3, 3, internal capsule; 4, 4, corona radiata; 5, optic thalamus; 6, lenticular nucleus; 7, corpus callosum.

In the human subject, lesions affecting the anterior two-thirds of the posterior division of the internal capsule produce paralysis of motion only, and are followed by descending degenerations. The fibres in this part are connected with the corpora striata. Lesions affecting both the anterior two-thirds and the posterior third of the posterior division of the internal capsule produce paralysis of motion and sensation. The fibres in the posterior third are connected with the optic thalami. Ascending degenerations have not been observed in the fibres of the cerebrum.

*Tubercula Quadrigemina.*—These little bodies, sometimes called the optic lobes, are rounded eminences, two upon either side, situated just below the third ventricle. The anterior, called the nates, are the larger. These are oblong, and of a grayish color externally. The posterior, called the testes, are situated just behind the anterior. They are rounded and are rather lighter in color than the anterior. Both contain gray nervous matter in their interior. They are the main points of apparent origin of the optic nerves and are connected by commissural fibres with the optic thalami. In birds the tubercles are two in number, instead of four, and are called tubercula bigemina. The anatomical and physiological relations of these bodies will be fully described in connection with the sense of sight.

*Crura Cerebri.*—The crura are short, thick, rounded bands which pass from the cerebral hemispheres to the upper border of the pons Varolii.

They are rather broader above than below and are about three-quarters of an inch (19 mm.) in length. They are composed of longitudinal white fibres connecting various parts with the cerebrum. Each crus is divided into a superficial and a deep band, by a layer of gray substance called the locus niger. The locus niger contains small, multipolar nerve-cells and abundant pigmentary granules. The lower, or superficial band of the crus is called the crusta. The deep band is called the tegmentum. The crusta consists of white fibres only. In the tegmentum the fibres are mixed with masses of gray matter.

*Pons Varolii.*—The pons Varolii, called the tuber annulare or the mesocephalon, is situated at the base of the brain, just above the medulla oblongata. It is white externally and contains in its interior a large admixture of gray matter. It presents both transverse and longitudinal white fibres. Its transverse fibres connect the two halves of the cerebellum. Its longitudinal fibres are connected below with the anterior pyramidal bodies and the olivary bodies of the medulla oblongata, the lateral columns of the cord and a certain portion of the posterior columns. The fibres are connected above with the crura cerebri and pass to the brain. The superficial transverse fibres are wanting in animals in which the cerebellum has no lateral lobes.

If the cerebral hemispheres, the olfactory ganglia, the optic lobes, the corpora striata and the optic thalami be removed, the animal loses the special senses of smell and sight and the intellectual faculties, there is a certain degree of enfeeblement of the muscular system, but voluntary motion and general sensibility are retained. As far as voluntary motion is concerned, an animal operated upon in this way is in nearly the same condition as one simply deprived of the cerebral hemispheres. There are no voluntary movements which show any degree of intelligence, but the animal can stand, and various consecutive movements are executed, which are different from the simple reflex acts depending exclusively upon the spinal cord. The co-ordination of movements is perfect, unless the cerebellum be removed. As regards general sensibility, an animal deprived of all the encephalic ganglia, except the pons Varolii and the medulla oblongata, undoubtedly feels pain. This has been demonstrated by Longet, Vulpian and others. In rabbits, rats and other animals, after removal of the cerebrum, corpora striata and optic thalami, pinching of the ear or foot is immediately followed by prolonged and plaintive cries. Both Longet and Vulpian have insisted upon the character of these cries as indicating the actual perception of painful impressions, and as very different from cries that are purely reflex, according to the ordinary acceptation of this term. Longet alluded to the voluntary movements and the cries observed in persons subjected to painful surgical operations, when incompletely under the influence of an anæsthetic, concerning the character of which there can be no doubt. He regarded the movements as voluntary, and the cries as evidence of the acute perception of pain; but it is well known that such patients have no recollection of any painful impression, although they have apparently experienced great suffering. As far as can be judged from what is positively known of the action of the encephalic centres, the pain under these conditions is perceived by some nerve-centre, probably in the pons Varolii, but the impression is not conveyed to the cerebrum and is not recorded by the memory.

Taking all the experimental facts into consideration, the following seems to be the most reasonable view with regard to the action of the pons Varolii as a nerve-centre:

It is an organ capable of originating impulses giving rise to voluntary movements, when the cerebrum, corpora striata and the optic thalami have been removed, and it probably regulates the automatic voluntary movements of station and progression. Many voluntary movements, the result of intellectual effort, are made in obedience to a stimulus transmitted from the cerebrum, through conducting fibres in the pons Varolii, to the motor conductors of the cord and the general motor nerves.

The gray matter of the pons Varolii is also capable of perceiving painful impressions, which, when all of the encephalic ganglia are preserved, are conducted to and are perceived by the cerebrum, and are remembered; but there are distinct evidences of the perception of pain, even when the cerebrum has been removed.

*Directions of the Fibres in the Cerebrum.*—Fibres pass from the cerebral hemispheres to the cerebellum. Commissural fibres connect the cerebrum and certain of the basal ganglia on the two sides. Fibres connect the gray matter of the cerebral convolutions on the same side with each other. Fibres pass from the inner surface of the gray matter of the cerebrum to the internal capsule, corpora striata, optic thalami and pons Varolii, to the medulla oblongata and thence to the spinal cord. The directions of these four sets of fibres have been quite accurately described.

1. *Fibres connecting the Cerebrum with the Cerebellum.*—(A) Fibres from the gray matter of the frontal lobe, in front of the anterior central convolution, pass through the anterior division of the internal capsule and thence through the inner portion of the outer layer of the crus cerebri (crusta) to the pons Varolii, where they seem to go to the cells of the gray matter. From the pons, fibres go to the lateral and posterior regions of the cerebellum on the opposite side. This connection, therefore, is crossed. (B) Fibres from the occipital and temporo-sphenoidal lobes of the cerebrum pass in the outer portion of the crusta and go to the upper portion of the cerebellum, near the middle lobe. This connection is probably crossed. (C) Above the pyramidal tract of the crusta, is a small tract of fibres which connect the caudate nucleus of the corpus striatum with the cerebellum (Gowers).

2. *Fibres connecting the Two Sides of the Brain.*—(A) Fibres coming from the inner surface of the gray matter of the cerebral convolutions pass from one side to the other, through the corpus callosum, and connect the two cerebral hemispheres with each other. These are the transverse fibres of the corpus callosum. (B) Fibres from the gray matter of the temporo-sphenoidal lobe on either side pass through the corpora striata to the anterior commissure. These fibres connect the temporo-sphenoidal lobes, and probably

also the corpora striata, on the two sides. (C) Fibres from the deeper portion of the crus cerebri (tegmentum) pass to the optic thalamus on either side and thence to the temporo-sphenoidal lobes. These fibres form the posterior commissure and connect the temporo-sphenoidal lobes and the optic thalami of the two sides.

3. *Fibres connecting Different Cerebral Convolutions on the same Side.*—(A) The so-called arcuate fibres, passing in a curved direction from one convolution to another, connect adjacent convolutions. (B) Other fibres, called longitudinal or collateral fibres, connect distant convolutions with each other. The fibres of the fornix connect the optic thalamus with the hippocampus major and the unicate gyrus. Fibres in the corpus callosum connect the anterior and posterior extremities of the gyrus fornicatus. These are the longitudinal fibres of the corpus callosum. Other longitudinal fibres, connecting parts more or less distant from each other, are found in the tænia semicircularis, the unicate fasciculus, the fillet of the gyrus fornicatus and the inferior longitudinal fasciculus. The last-mentioned fasciculus connects the gray matter of the temporo-sphenoidal and occipital lobes.

4. *Fibres connecting the Brain with the Spinal Cord.*—If these fibres be followed from the cortex of the brain downward, they are called converging, and if they be followed from below upward, they are called radiating fibres.

Arising from the internal, concave surface of the cortical substance of the cerebrum, the converging fibres, at first running side by side with the curved, commissural fibres, separate from the latter as they curve backward to pass again to the cortical substance, and are directed toward the corpora striata and the optic thalami. The limits of the irregular planes of separation of the commissural and the converging fibres contribute to form the boundaries of the ventricular cavities of the brain. In studying the course of the converging fibres arising from all points in the concave surface of the cerebral gray matter, it is found that they take various directions. The fibres from the anterior region of the cerebrum pass backward and form distinct fasciculi which converge to the gray substance of the corpora striata. The fibres from the middle portion converge regularly to the middle region of the external portions of the optic thalami. The fibres from the posterior portion pass from behind forward and are distributed in the posterior portion of the optic thalami. The fibres from the convolutions of the hippocampi and the fascia dentata are lost in the gray substance lining the internal borders of the optic thalami In the course of most of these fibres toward the corpora striata and the optic thalami, they pass through the internal capsule.

The fibres from the anterior and middle portions of the cerebrum, especially the middle portion, contribute largely to the formation of the anterior two-thirds of the posterior division of the internal capsule. The fibres from the posterior portion of the cerebrum are found in the posterior third of the posterior division of the internal capsule. The posterior fibres are probably sensory. The middle and anterior fibres are motor. The latter undergo descending degenerations following lesions of the anterior and posterior central convolutions (Charcot). A few of the converging fibres from the hemispheres pass directly through the internal capsule and have no connection with the corpora striata and optic thalami.

From the internal capsule, the fibres pass in the crus cerebri to the upper border of the pons Varolii. The motor fibres pass through the pons as lon-

FIG. 225.—*Diagrammatic representation of the direction of some of the fibres in the cerebrum* (Le Bon).

gitudinal fibres, go to the anterior pyramids of the medulla oblongata, where most of them decussate, and thence to the pyramidal tracts of the spinal cord. The sensory fibres go to the posterior part of the cord. The converging cerebral fibres are re-enforced, in their downward course, by fibres from the tubercular quadrigemina and the gray matter of the pons Varolii. Certain fibres go to the olivary bodies in the medulla oblongata. A more extended description of these fibres will be given in connection with the physiological anatomy of the medulla.

*Cerebral Localization.*—The observations of Flourens (1822 and 1823) and his immediate followers, which seemed to show that the cerebrum was neither excitable nor sensible to direct stimulation, have been so completely contradicted by the experiments of Fritsch and Hitzig (1870), Ferrier, Munk, Horsley and many others, that the question of the existence of motor and sensory centres—especially motor centres—hardly admits of discussion. The negative results obtained by Flourens were probably due to severe hæmorrhage, which, according to Ferrier, rapidly destroys the excitability of the motor cortical areas. Some of the experiments of Goltz, by which it has been attempted to prove that circumscribed and invariable motor areas do not exist, are answered by observations showing descending secondary degenerations following injury of certain parts of the cerebral cortex. The earlier observations on cerebral localization were made on dogs. Later, experiments have been made on monkeys, and the results of these have been to a certain extent confirmed by pathological observations on the human subject. Beginning with the observations in which descending degenerations have been noted as a consequence of destruction of parts of the cerebral cortex, it may be assumed that a distinct area exists which presides over certain localized muscular movements.

*Motor Cortical Zone.*—The motor cortical zone is on either side of the fissure of Rolando. It is usually described as including the anterior and pos-

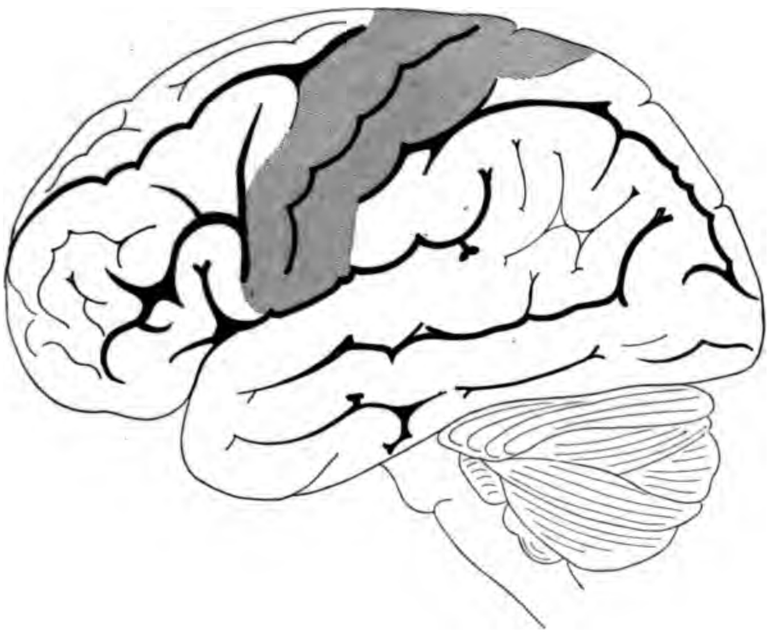


FIG. 226.—*Motor cortical zone, on the outer surface of the cerebrum* (Exner).

terior central convolutions (see Fig. 221) and the paracentral lobule (see Fig. 222). Faradization of parts in this zone is followed by localized muscular movements. In fact, the motor areas seem to be subject to nearly the same laws, as regards their reactions to Faradic stimulation, as are the motor nerves. Forty Faradic shocks per second produce a corresponding number of single muscular contractions. Forty-six shocks per second produce a tetanic contraction (Franck and Pitres). Destruction of motor areas is followed by partial loss of power in certain sets of muscles, and by descending secondary degeneration of nerve-fibres, extending through the corona radiata, the internal capsule, the crura cerebri, the anterior pyramids of the medulla oblongata and finally the pyramidal tracts of the spinal cord.

It remains now to locate the distinct motor areas. This has been done on the brain of the monkey, by Ferrier, who has applied his observations as

FIG. 227.—*Paracentral lobule, on the inner surface of the cerebrum* (Exner). The shaded area in the diagram is the paracentral lobule.

nearly as possible to the human brain. While the divisions made by Ferrier can not be taken as absolute, experiments on monkeys have been followed by

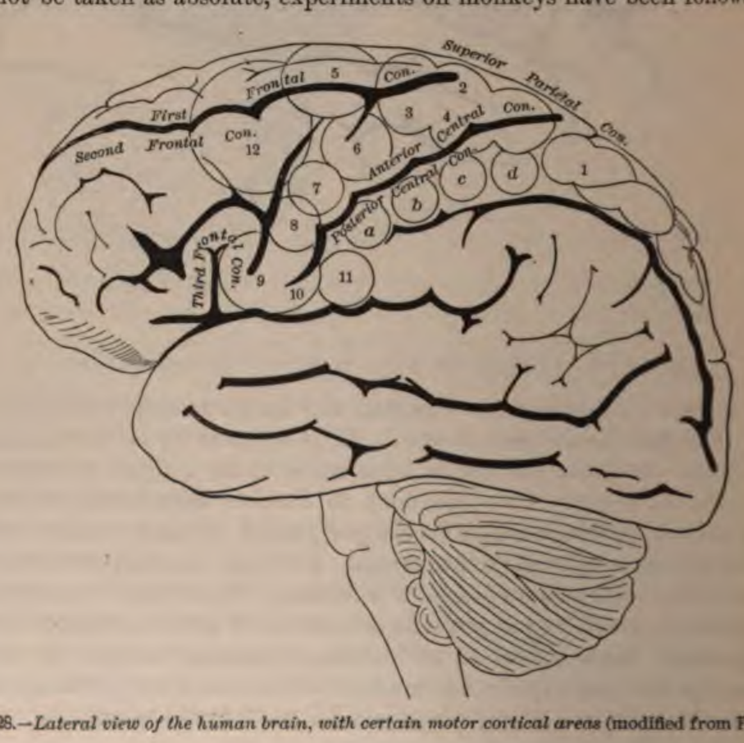



FIG. 228.—*Lateral view of the human brain, with certain motor cortical areas* (modified from Ferrier).

results so nearly constant, that the localizations may be accepted as nearly correct. In the diagram (Fig. 228) and descriptions, the centres for the special senses have been omitted, to be taken up in connection with the physiology of olfaction, vision, audition and gustation.

In the following description, the numbers and letters refer to Fig. 22:

(1). This, which is on the precuneus (compare Fig. 222), indicates the position of the centres for movements of the opposite leg and foot, such as are concerned in locomotion.

(2), (3), (4). These numbers, which are over the convolutions bounding the upper extremity of the fissure of Rolando (including the paracentral lobule—compare Fig 222), include centres for various complex movements of the arms and legs, such as are concerned in climbing, swimming, etc.

(5) Situated at the posterior extremity of the first frontal convolution, at its junction with the anterior central convolution, is the centre for the extension forward of the arm and hand, as in putting forth the hand to touch something in front.

(6) Situated on the anterior central convolution, just behind the upper end of the posterior extremity of the second frontal convolution, is the centre for the movements of the hand and forearm, in which the biceps is particularly engaged; viz., supination of the hand and flexion of the forearm.

(7), (8). Just below (6), on the anterior central convolution, are centres respectively for the elevators and depressors of the mouth.

(9), (10). These numbers taken together, on the third frontal convolution, mark the centre for the movements of the lips and tongue, as in articulation. "This is the region, disease of which causes aphasia, and is generally known as Broca's convolution."

(11). This, which is on the lower end of the posterior central convolution, marks "the centre of the platysma, retraction of the angle of the mouth."

(12) This, which is on the posterior part of the first and second frontal convolution, marks "a centre for lateral movements of the head and eyes, with elevation of the eyelids and dilatation of pupil."

(*a*), (*b*), (*c*), (*d*). These letters, on nearly the whole of the posterior central convolution, "indicate the centres of movement of the hand and wrist."

The above description is quoted from Ferrier, with certain changes in the nomenclature of the convolutions. Schäfer and Horsley in the main have confirmed and have somewhat extended the researches of Ferrier. These observers have shown that the centres on the outer surface of the cerebrum, near the great longitudinal fissure, extend to the inner surface. In the first frontal convolution, in front of the paracentral lobule, is a centre for movements of the trunk (Tr., Fig. 229), and in front of this, is a centre for the movements of the arm and shoulder. Other parts of the inner cerebral surface, except the paracentral lobule, are inexcitable.

In man lesions of parts of the motor-cortical zone produce localized paralysis, or what is called monoplegia, the action being crossed. "The following forms of monoplegia have been observed to attend localized cortical lesions: 1, oculo-motor monoplegia (isolated ptosis); 2, facial monoplegia, sometimes combined with paralysis of the hypoglossal nerve; 3, brachial monoplegia, or paralysis of the opposite arm; 4, crural monoplegia, or paralysis of the opposite leg; 5, brachio-facial monoplegia, or paralysis of the arm and face" (Flint's "Practice of Medicine").

FIG. 229.—*Inner surface of the right cerebral hemisphere* (Schäfer and Horsley).
A. S., area governing the movements of the arm and shoulder; Tr., area for movements of the trunk; LEG. (paracentral lobule) area for movements of the leg.

It is possible that there may be sensory centres in the cerebral cortex, but they have not been satisfactorily localized, although attempts have been made to limit such areas by studying reflex phenomena following stimulation of certain parts. It may be stated in general terms that the occipital and temporo-sphenoidal lobes, the fibres from which pass through the posterior third of the posterior division of the internal capsule, are specially connected with sensation.

One of the most important of the cerebral centres is the centre for speech, which will be fully described after the consideration of the general uses of the cerebral hemispheres.

## GENERAL USES OF THE CEREBRUM.

The cortical gray substance of the cerebral hemispheres not only is capable of generating motor impulses of the kind known as voluntary, and of receiving sensory impressions, including those connected with the special senses, but its anatomical and physiological integrity, and its connections, especially with sensory conductors, are essential to what are known as mental operations. The existence of the mind and the possibility of normal operations of the intelligence depend upon the existence of the gray matter of the cerebral cortex and its normal physiological condition and relations. This proposition does not imply that the mind is a force which operates through the brain, or even, strictly speaking, that the brain is the seat of the intellectual faculties. Mental operations involve a slight elevation of temperature and slightly increase some of the excretions. It is probable, therefore, that they involve changes of matter; and these changes, if they occur, can be effected only by the cells of the brain. Without defining or analyzing the intellectual faculties or attempting to locate different faculties in special parts, it is sufficient to state that certain of these faculties reside probably in that portion of the brain which is anterior to the motor cortical zone; that is, in the frontal lobes. These lobes, as far as is known, do not present motor or sensory areas.

The brain and the intellectual power of man are so far superior in their development to this organ and its properties in the lower animals, that some philosophers have regarded the human intelligence as distinct in nature as well as in degree. Although physiologists do not generally accept this proposition, regarding the intelligence of man as simply superior in degree to that of the lower animals, it is evident that this difference in the degree of development is so great as to render the human mind hardly comparable with the intellectual attributes of animals low in the scale. Still, there can be no doubt with regard to the identity of the nature of the faculties of the brain in man and in some of the lower animals, however much these faculties may differ in their degree of development. If this proposition be true, it is reasonable to apply experiments on the brain in the lower animals to the physiology of corresponding parts in the human subject.

*Extirpation of the Cerebrum.*—Experiments upon different classes of animals show clearly that the brain is less important, as regards the ordinary manifestations of animal life, in proportion as its relative development is smaller. For example, if the cerebral hemispheres be removed from fishes or reptiles, the movements which are called voluntary may be but little affected; while if the same mutilation be performed in birds or some of the mammalia, the diminished power of voluntary motion is much more marked. It would be plainly unphilosophical to assume, because a fish or a frog will swim in water and execute movements after removal of the hemispheres very like those of the uninjured animal, that the feeble intelligence possessed by these animals is not destroyed by the operation. It is not only possible but probable that in the very lowest of the vertebrates, the operations of the nervous centres are not the same as in higher animals. There is, for example, a fish (the lancet-fish, *Amphioxus lanceolatus*), that has no brain, all of the functions of animal life being regulated by the gray substance of the spinal cord. It is essential, therefore, in endeavoring to apply the results of experiments upon the brain in the lower animals to human physiology, to isolate, as far as possible, the distinct manifestations of intelligence from automatic movements.

Flourens (1822 and 1823) made a series of important observations upon the different parts of the encephalon. As regards the cerebral hemispheres, he found that the complete removal of these parts in living animals (frogs, pigeons, fowls, mice, moles, cats and dogs), was invariably followed by stupor, apparent loss of intelligence and absence of even the ordinary instinctive acts. Animals thus mutilated retained general sensibility and the power of voluntary movements, but were thought to be deprived of the special senses of sight, hearing, smell and taste. As regards general sensibility and voluntary movements, Flourens was of the opinion that animals deprived of their cerebral lobes possessed sensation, but had lost the power of perception, and that they could execute voluntary movements when an irritation was applied to any part, but had lost the power of making such movements in obedience to an effort of the will. One of the most remarkable phenomena observed was entire loss of memory and of the power of connecting ideas. The voluntary muscular system was enfeebled but not paralyzed. Removal of one hemisphere produced, in the higher classes of animals experimented upon, enfeeblement of the muscles upon the opposite side, but the intellectual faculties were in part or entirely retained.

The observations of Flourens have been repeated by many physiologists, and were in the main confirmed, except as regards the special senses. Bouillaud (1826) made a large number of observations upon pigeons, fowls, rabbits and other animals, in which, after removal of the hemispheres, he noted the persistence of the senses of sight and hearing. Longet finally demonstrated the fact that both sight and hearing are retained after extirpation of the hemispheres, even more clearly than Bouillaud, by the following experiments: He removed the hemispheres from a pigeon, the animal surviving the operation eighteen days. When this animal was placed in a dark room and a light was suddenly brought near the eyes, the iris contracted and the animal winked; "but it was remarkable, that when a lighted candle was moved in a circle, and at a sufficient distance, so that there should be no sensation of heat, the pigeon executed an analogous movement of the head." An examination after death showed that the removal of the cerebrum had been complete. An animal deprived of the hemispheres also opened the eyes at the report of a pistol and gave other evidence that the sense of hearing was retained.

With regard to the senses of smell and taste, it is more difficult to determine their presence than to ascertain that the senses of sight and hearing are retained. It is probable, however, that the sense of smell is not abolished, if the hemispheres be carefully removed, leaving the olfactory ganglia intact; and there is no direct evidence that extirpation of the cerebrum affects the sense of taste; indeed, in young cats and dogs, Longet has noted evidences of a disagreeable impression following the introduction of a concentrated solution of colocynth into the mouth, as distinctly as in the same animals under normal conditions.

*Comparative Development of the Cerebrum in the Lower Animals.*—It is only necessary to refer very briefly to the development of the cerebrum in the lower animals as compared with the human subject, to show the connection of the hemispheres with intelligence. In man the cerebrum presents a large preponderance in weight over other portions of the encephalon; and in some of the lower animals the cerebrum is even less in weight than the cerebellum. In man, also, not only the relative but the absolute weight of the brain is greater than in lower animals, with but two exceptions. Todd has cited a number of observations made upon the brains of elephants, in which the weights ranged between nine and ten pounds (about 4,000 and 4,500 grammes). Rudolphi gave the weight of the encephalon of a whale, seventy-five feet long (about 23 metres), as considerably over five pounds (about 2,300 grammes). With the exception of these animals, man possesses the largest brain in the zoölogical scale.

Another interesting point in this connection is the development of cerebral convolutions in certain animals, by which the relative quantity of gray matter is increased. In fishes, reptiles and birds, the surface of the hemispheres is smooth; but in many mammalia, especially in those remarkable for intelligence, the cerebrum presents a greater or less number ot convolutions, as it does in the human subject.

*Development of the Cerebrum in Different Races of Men and in Different Individuals.*—It may be stated as a general proposition, that in the different races of men, the cerebrum is developed in proportion to their intellectual power; and in different individuals of the same race, the same general rule obtains. Still, this law presents marked exceptions. Certain brains in an inferior race may be larger than the average in the superior race; and it is frequently observed that unusual intellectual vigor is co-existent with a small brain, and the reverse. These exceptions, however, do not take away from the force of the original proposition. As regards races, the rule is found to be invariable, when a sufficient number of observations are analyzed, and the same holds true in comparing a large number of individuals of the same race. Average men have an advantage over average women of about six ounces (170 grammes) of cerebral substance; and while many women are far superior in intellect to many men, such instances are not sufficiently frequent to invalidate the general law, that the greatest intellectual capacity and mental vigor is coincident with the greatest quantity of cerebral substance. If the view, which is in every way reasonable, be accepted, that the gray substance alone of the cerebral hemispheres is directly connected with the mind, it would be necessary, in comparing different individuals with the view of establishing a definite relation between brain-substance and intelligence, to estimate the quantity of gray matter; but it is not easy to see how this can be done with any degree of accuracy.

It is undoubtedly true that proper training and exercise develop and increase the vigor of the intellectual faculties, and that thereby the brain is increased in power, as are the muscles under analogous conditions. This will perhaps explain some of the exceptions above indicated; but an additional explanation may be found in differences in the quality of brain-substance in different individuals, irrespective of the size of the cerebral hemispheres. One evidence that these differences in the quality of intellectual working matter exist, is that some small brains actually accomplish more and better work than some large brains. This fact may be due to differences in training, to the extraordinary development, in some individuals, of certain qualities, to intensity and pertinacity of purpose, capacity for persistent labor in certain directions, a fortunate direction of the mental efforts, opportunity and circumstances, etc.; but aside from these considerations, it is exceedingly probable that there are important individual differences in the quality of nervous matter.

*Facial Angle.*—It is not necessary to enter into an extended discussion of the relations of the facial angle to intelligence. It was proposed by Camper to take the angle made at the junction of two lines, one drawn from the most projecting part of the forehead to the alveolæ of the teeth of the upper jaw, and another passing horizontally backward from the lower extremity of the first line, as the facial angle. This angle is to a certain extent a measure of the projection of the anterior lobes of the brain. A number of observations upon the facial angle in different races has been made by Camper and by other physiologists and ethnologists. These show, in general terms, that the angle is larger in man than in any of the inferior animals and is largest in those races that possess the greatest intellectual development.

*Pathological Observations.*—It is a fact now generally admitted in pathology, that loss of cerebral substance from repeated hæmorrhage is sooner or later followed by impairment of the intellectual faculties. This point is frequently difficult to determine in an individual instance, but an analysis of a sufficient number of cases shows impaired memory, tardy, inaccurate and feeble connection of ideas, abnormal irritability of temper with a childish susceptibility to petty or imaginary annoyances, easily excited emotional manifestations and a variety of phenomena denoting abnormally feeble intellectual power, following any considerable disorganization of cerebral substance. In short, pathological conditions of the brain all go to show that the intellectual faculties are directly connected with the cerebral hemispheres.

In idiots the brain usually is of small size, although there are exceptions to this rule. In two cases of adult idiots, reported by Tiedemann, the brain was about one-half of the normal weight. The brain of an idiotic woman, forty-two years of age, reported by Gore, weighed ten ounces and five grains (about 284 grammes). It has been observed, also, that the cerebellum is not proportionally diminished in size in idiots (Bradley). In one instance reported, the proportion of the cerebellum to the cerebrum was as 1 to 5·5. In the healthy adult male of ordinary weight, the proportion is as 1 to 8⅐. The statements just made with regard to the brains of idiots refer to cases characterized by complete absence of intelligence, and farthermore, probably, by very small development of the body. On the other hand, there are instances of idiocy, the body being of ordinary size, in which the weight of the encephalon is little if any below the average. Lélut has reported several cases of this kind. In one of these, a deaf-mute idiot, forty-three years of age, a little above the ordinary stature, presenting "idiocy of the lowest degree; almost no sign of intelligence; no care of cleanliness," the encephalon weighed 48·32 oz. (1,369·8 grammes). Other cases of idiots of medium stature are given, in which the brain weighed but little less than the normal average. In the *West Riding Lunatic Asylum Reports*, London, 1876, is a report of the case of a congenital imbecile, aged thirty years, height five feet and eight inches (172·7 centimetres), died of phthisis, whose brain weighed 70½ oz. (2,000 grammes). This is heavier than the heaviest normal brain on record. The normal brain-weight is 49½ oz. (1,408·3 grammes).

*Reaction-Time.*—The time which elapses between the application of a stimulus and its appreciation by the individual experimented upon is known as reaction-time. In experiments with reference to this point, the person observed makes an electric signal when the sensation is perceived. The reaction time is 0·12 of a second for a shock on the hand, 0·13 for the forehead, 0·17 for the toe and 0·13 for a sudden noise (Exner). The duration is about 0·16 of a second for impressions made on the nerves of special sense. This is the time of conduction of the impression to the brain, its appreciation by the individual, the generation of the voluntary impulse and the conduction of this impulse to the muscles concerned in making the signal. It is probably subject to variations analogous to those observed in the "personal equation."

*Centre for the Expression of Ideas in Language.*—The location of this centre depends entirely upon the study of cases of disease in the human subject. It is evident that there must be a comprehension of the significance of words, the formation of an idea more or less complex, and a co-ordinate action of the muscles concerned in speech, as conditions essential to expression in spoken words. One or more of these conditions may be absent in cases of disease; and the general absence of the power of verbal expression, when this depends on cerebral lesion, is known as aphasia. This is quite different from aphonia, which is simply loss of voice. If the comprehension of the meaning of words be absent, the individual is incapable of receiving ideas expressed in language. In cases of aphasia it often is difficult to determine this point. In certain cases it is possible that the individual may understand what is said and may form ideas to which he is unable to give verbal expression. In such instances he can neither speak nor write. There are certain cases in which the written or printed words convey no idea, while spoken words are understood, but there is no loss of intelligence and words are spoken without difficulty. This condition is called word-blindness. If there be simple want of co-ordination of the muscles concerned in speech, words are spoken which may have no connection with the idea to be conveyed, but the individual may be able to express himself in writing. This condition is known as ataxic aphasia. The inability to express ideas in writing is called agraphia, and this is usually an indication of the condition known as amnesic aphasia, in which it is impossible to put ideas into words in any way. Persons affected with purely ataxic aphasia may understand and write perfectly, but they can not read aloud or repeat words or sentences spoken to them. In cases of simple amnesic aphasia, patients can sometimes repeat dictated words. In cases in which hemiplegia is marked, the aphasia usually is ataxic. In cases in which there is no hemiplegia, the aphasia usually is amnesic. The ataxic and amnesic forms of aphasia may be combined. A full description, however, of the many and varied forms of aphasia would be out of place in this work.

In 1766, Pourpour du Petit reported a case of aphasia, with lesion of the left frontal lobe of the cerebrum, in which the patient could pronounce nothing but "*non.*"

Marc Dax (1836) indicated loss or impairment of speech in one hundred and forty cases of right hemiplegia. These observations attracted little attention, until 1861, when the subject was studied by Broca. Since then, many cases of aphasia with lesion of the left frontal lobe have been reported by various writers. In 1863, M. G. Dax, a son of Marc Dax, limited the lesion to the middle portion of the left frontal lobe. It was farther stated, by Broca and Hughlings Jackson, to be that portion of the brain nourished by the left middle cerebral artery (the inferior frontal branch). According to recent observers, the most frequent lesion is in the parts supplied by the left middle cerebral artery, particularly the lobe of the insula, or the island of Reil; and it is a curious fact that this part is found only in man and monkeys, being in the latter very slightly developed.

While the cerebral lesion in aphasia involves the left frontal lobe in the great majority of cases, there are instances in which the right lobe alone is affected, and these occur in left-handed persons. Aside from the anatomical arrangement of the arteries, which seem to furnish a greater quantity of blood to the left hemisphere, it is evident that as far as voluntary movements are concerned, the right hand, foot, eye etc., are used in preference to the left, and that the motor operations of the left hemisphere are superior in activity to those of the right. Bateman has quoted two cases of aphasia dependent upon lesion of the right side of the brain, and consequent left hemiplegia, in which the persons were left-handed; and these, few as they are, are important, as showing that a person may use the right side of the brain in speech, as in the other motor acts. Although most anatomists have failed to find any considerable difference in the weight of the two cerebral hemispheres, Boyd has shown by an "examination of nearly two hundred cases at St. Marylebone, in which the hemispheres were weighed separately, that almost invariably the weight of the left exceeded that of the right by at least the eighth of an ounce (4·5 grammes)."

Broadbent has reported an examination of the encephalon of a deaf and dumb woman. In this case the brain was found to be of about the usual weight, but the left third frontal convolution was of "comparatively small size and simple character."

Taking into consideration all of the pathological facts bearing upon the question, it seems certain that in the great majority of persons, the organ or part presiding over the faculty of language is situated on the left side, at or near the third frontal convolution and the island of Reil, mainly in the parts supplied by the middle cerebral artery. In some few instances the organ seems to be in the corresponding part upon the right side. It is possible that originally both sides preside over speech, and the superiority of the left side of the brain over the right and its more constant use by preference in right-handed persons may lead to a gradual abolition of the action of the right side of the brain, in connection with speech, simply from disuse. This view, however, is purely hypothetical. In some cases of aphasia from lesion of the speech-centre in the left hemisphere, recovery takes place, and occasionally "speech has been again lost when a fresh lesion occurred in this part of the right hemisphere" (Gowers). In the ataxic form of aphasia, the idea and memory of words remain, and there is loss of speech simply from inability to co-ordinate the muscles concerned in articulate language. Patients affected in this way can not speak but can write with ease and correctness. In the amnesic form of the disease, the idea and memory of language are lost; patients can not speak, and are affected with agraphia, or inability to write. The motor tracts from the centre for speech pass to the anterior portion of the posterior division of the internal capsule and thence through the left crus, into the pons Varolii, where they decussate and go to the right side of the medulla oblongata.

## THE CEREBELLUM.

It is not necessary in order to comprehend the uses of the cerebellum, as far as these are known, to enter into a full description of its anatomical characters. The points, in this connection, that are most important are the following: the division of the substance of the cerebellum into gray and white matter; the connection between the cells and the fibres; the connection of the fibres with the cerebrum and with the prolongations of the columns of the spinal cord; the passage of fibres between the two lateral lobes. These are the only anatomical points that will be considered.

*Physiological Anatomy.*—The cerebellum, situated beneath the posterior lobes of the cerebrum, weighs about 5·25 ounces (148·8 grammes) in the male, and 4·7 ounces (135 grammes) in the female. The proportionate weight to that of the cerebrum is as 1 to 8¾ in the male, and as 1 to 8¼ in the female. The cerebellum is separated from the cerebrum by a strong process of the dura mater, called the tentorium. Like the cerebrum, the cerebellum presents an external layer of gray matter, the interior being formed of white, or fibrous nerve-tissue. The extent of the gray substance is much increased by abundant, fine convolutions and is farther extended by the penetration, from the surface, of arborescent processes of gray matter. Near the centre of each lateral lobe, embedded in the white substance, is an irregularly dentated mass of gray matter, called the corpus dentatum. The convolutions are finer and more abundant and the gray substance is deeper in the cerebellum than in the cerebrum. These convolutions, also, are present in many of the inferior animals in which the surface of the cerebrum is smooth.

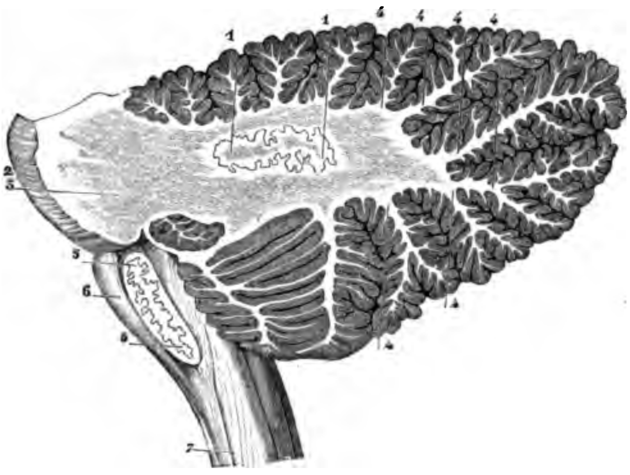



FIG. 230.—*Cerebellum and medulla oblongata* (Hirschfeld).
1, 1, corpus dentatum; 2, pons Varolii; 3, section of the middle peduncle; 4, 4, 4, 4, 4, 4, laminæ forming the arbor vitæ; 5, 5, olivary body of the medulla oblongata; 6, anterior pyramid of the medulla oblongata; 7, upper extremity of the spinal cord.

The cerebellum consists of two lateral hemispheres, more largely developed in man than in the inferior animals, and a median lobe. The hemispheres are subdivided into smaller lobes, which it is unnecessary to describe. Beneath the cerebellum, bounded in front and below by the medulla oblongata and pons Varolii, laterally, by the superior peduncles, and above, by the cerebellum itself, is a lozenge-shaped cavity, called the fourth ventricle. The crura, or peduncles, will be described in connection with the direction of the fibres.

The gray substance of the convolutions is divided quite distinctly into an internal and an external layer. The internal layer presents an exceedingly delicate net-work of fine nerve-fibres which pass to the cells of the external layer. The external layer is somewhat like the external layer of gray substance of the posterior lobes of the cerebrum and is more or less sharply divided into two or more secondary layers. The most external portion of this layer contains a few small nerve-cells and fine filaments of connective tissue. The rest of the layer contains a great number of large cells, rounded or ovoid, with two or three and sometimes four prolongations. The mode of connection between the nerve-cells and the fibres has already been described under the head of the general structure of the nervous system.

*Directions of the Fibres in the Cerebellum.*—Fibres from the gray substance of the convolutions and their prolongations, and from the corpus dentatum, converge to form the three cerebellar peduncles on either side. The superior peduncles pass forward and upward to the crura cerebri and the optic thalami. These connect the cerebellum with the cerebrum. Beneath the tubercular quadrigemina, some of these fibres decussate with the corresponding fibres from the opposite side; so that certain of the fibres of the superior peduncles pass to the corresponding side of the cerebrum and others pass to the cerebral hemisphere of the opposite side. The connections between the cerebrum and the cerebellum, through the pons Varolii, have already been described (see page 610).

The middle peduncles arise from the lateral hemispheres of the cerebellum, pass to the pons Varolii, where they cross, connecting the two sides of the cerebellum.

The inferior peduncles pass to the medulla oblongata and are continuous with the restiform bodies, which, in turn, are continuations chiefly of the posterior columns of the spinal cord.

From the above sketch, the physiological significance of the direction of the fibres is sufficiently evident. By the superior peduncles, the cerebellum is connected, as are all of the encephalic ganglia, with the cerebrum; by the middle peduncles, the two lateral halves of the cerebellum are intimately connected with each other; and by the inferior peduncles, the cerebellum is connected with the posterior columns of the spinal cord.

*Extirpation of the Cerebellum.*—When the greatest part or the whole of the cerebellum is removed from a bird or a mammal, the animal being, before the operation, in a perfectly normal condition and no other parts being injured, there are no phenomena constantly and invariably observed except certain modifications of the voluntary movements (Flourens). The intelligence, general and special sensibility, the involuntary movements and the simple faculty of voluntary motion remain. The movements are always exceedingly irregular and inco-ordinate; the animal can not maintain its equilibrium; and on account of the impossibility of making regular movements, it can not feed. This want of equilibrium and of the power of co-ordinating the muscles of the general voluntary system causes the animal to assume the most absurd and remarkable postures, which, to one accustomed to these experiments, are entirely characteristic. Calling this want of equilibration, of co-ordination, of "muscular sense," an indication of vertigo, or by any other name, the fact remains, that regular and co-ordinate muscular action in standing, walking or flying, is impossible, although voluntary power is retained. It is well known that many muscular acts are more or less automatic, as in standing, and to a certain extent, in walking. These acts, as well as nearly all voluntary movements, require a certain co-ordination of the muscles, and this, and this alone, is affected by extirpation of the cerebellum. It is true that destruction of the semicircular canals of the internal ear produces analogous disorders of movement, but this is the only mutilation, except division of the posterior white columns of the spinal cord, which produces anything resembling the results of cerebellar injury.

When a portion only of the cerebellum is removed, there is slight disturbance of co-ordination, and the disordered movements are marked in proportion to the extent of the injury. After extirpation of even one-half or two-thirds of the cerebellum, the disturbances in co-ordination immediately following the operation may disappear, and the animal may entirely recover, without any regeneration of the extirpated nerve-substance. This important fact enables one to understand how, in certain cases of disease of the cerebellum in the human subject, when the disorganization of the nerve-tissue is slow and gradual, there may never be any disorder in the movements.

If there be a distinct nerve-centre which presides over the co-ordination of the general voluntary movements, experiments upon the higher classes of animals show that this centre is situated in the cerebellum. If the cerebellum preside over co-ordination, as a physiological necessity, the centre must be connected by nerves with the general muscular system. If this connection exist, a complete interruption of the avenue of communication between the cerebellum and the muscles would be followed by loss of co-ordinating power. From the anatomical connections of the cerebellum, it appears that the main communication between this organ and the general system is through the posterior white columns of the spinal cord. These columns are not for the transmission of the general sensory impressions, and there is no satisfactory evidence that they convey to the encephalon the so-called muscular sense. When the posterior white columns are divided at several points, there is want of co-ordination of the general muscular system. When the posterior white columns are disorganized in the human subject, there is loss or impairment of co-ordinating power, even though the general sensibility be not affected, as in the disease called locomotor ataxia.

*Pathological Observations.*—Records of cases of lesion of the cerebellum in the human subject have accumulated until the number is very large. A study of cases in which the phenomena referable to cerebellar injury are not complicated by paralysis, coma or convulsions, shows that serious lesion of the middle lobe is almost always attended with marked muscular inco-ordination. Cases in which only a portion of one or of both hemispheres is involved may not present any disorder in the muscular movements. These facts are in accord with the results of experiments upon the lower animals.

The phenomena observed in the few cases of cerebellar inco-ordination which have been carefully observed are notably different from those presented in simple locomotor ataxia. In cerebellar disease, the gait is staggering, much as it is in alcoholic intoxication. The chief difficulty seems to be in maintaining the equilibrium in progression, even with the greatest care and closest attention on the part of the patient. With the idea in mind that there is a co-ordinating centre for the muscles of progression, and that this centre acts imperfectly, it seems as though an efficient effort at co-ordination were impossible. In locomotor ataxia, patients seem to make co-ordinating efforts, but the paths by which these efforts find their way to the muscles are disturbed and the co-ordinating process, which is more or less automatic in health, requires peculiar care and attention. By the aid of the sense of sight and by artificial supports, progression may be safely though irregularly accomplished. The movements are jerky, and each step seems to require a distinct act of volition. It is possible to imagine that in disorganization of the paths of co-ordination in the spinal cord, the co-ordinating centre may act in some degree through the motor paths in the direct and crossed pyramidal tracts of the cord. It is certain that the want of normal co-ordinating power is supplemented by ordinary voluntary acts and by the sense of sight.

Vertigo is not a necessary accompaniment of cerebellar ataxia. Disease of the semicircular canals of the internal ear (Ménière's disease) is attended with vertigo, and this is the main cause of the disturbances of equilibrium.

*Connection of the Cerebellum with the Generative Function.*—The fact that the cerebellum is the centre for equilibration and the co-ordination of certain muscular movements does not necessarily imply that it has no other office. The idea of Gall, that "the cerebellum is the organ of the instinct of generation," is sufficiently familiar; and there are facts in pathology which show a certain relation between this nerve-centre and the organs of generation, although the view that it presides over the generative function is not sustained by the results of experiments upon animals or by facts in comparative anatomy.

In experiments upon animals in which the cerebellum has been removed, there is nothing pointing directly to this part as the organ of the generative instinct. Flourens removed a great part of the cerebellum in a cock. The animal survived for eight months. It was put several times with hens and always attempted to mount them, but without success, on account of want of equilibrium. In this animal the testicles were enormous. This observation has been repeatedly confirmed, and there are no instances in which the cerebellum has been removed with apparent destruction of sexual instinct. In a comparison of the relative weights of the cerebellum in stallions, mares and geldings, Leuret found that, far from being atrophied, the cerebellum in geldings was even larger than in either stallions or mares.

In certain cases of disease or injury of the cerebellum, irritation of this part has been followed by persistent erection and manifest exaggeration of the sexual appetite, and in others, its extensive degeneration or destruction has apparently produced atrophy of the generative organs and total loss of sexual desire. Serres reported several cases in which irritation of the cerebellum was followed by satyriasis or nymphomania, but in other cases there were no symptoms referable to the generative organs. In the well known case reported by Combette, the patient had the habit of masturbation. Fisher, of Boston, reported (1838) two cases of diseased or atrophied cerebellum, with absence of sexual desire, and one case of irritation, with satyriasis. Similar instances have been given by other writers. The observations of Budge, in which mechanical irritation of the cerebellum was followed by movements of the uterus, testicles etc., have not been satisfactorily explained.

Although there are many facts in pathology which are opposed to the view that the cerebellum presides over the generative function, there are cases which show a certain connection between this portion of the central nervous system and the organs of generation in the human subject; but this is all that can be said upon this point. It is certain that the facts are not sufficiently definite and invariable to sustain the notion that the cerebellum is the seat of the sexual instinct.

It is not necessary to discuss the vague theories with regard to the uses of the cerebellum advanced by writers anterior to the publication of the observations of Flourens. There is no evidence that the cerebellum is the organ presiding over memory, the involuntary movements, general sensibility or the general voluntary movements. The only view that has any positive experimental or pathological basis is that it presides over equilibration and the co-ordination of certain muscular movements, and is, perhaps, in some way connected with the generative function.

## Medulla Oblongata (Bulb).

The medulla oblongata, or bulb, connects the spinal cord with the encephalic ganglia. It is composed of white and gray matter and presents, in its substance, a number of important nerve-centres. It is not necessary to give anything like a complete anatomical description of the medulla. Its most important conducting parts are those which are continuous with the columns of the cord and which pass to the cerebrum and cerebellum. The nuclei of origin of certain of the cranial nerves in the floor of the fourth ventricle have already been mentioned.

*Physiological Anatomy.*—The medulla oblongata is pyramidal in form, with its broad extremity above, and rests in the basilar groove of the occipital bone, extending from the lower border of the pons Varolii to the atlas. It is about an inch and a quarter (31·8 mm.) in length, three-quarters of an inch (19·1 mm.) broad at its widest portion and half an inch (12·7 mm.) thick. It is flattened antero-posteriorly. Like the cord, it has an anterior and a posterior median fissure.

Apparently continuous with the anterior columns of the cord, are the two anterior pyramids, one on either side. Viewed superficially, the innermost fibres of these pyramids are seen to decussate in the median line; but if the fibres be traced from the cord, it is found that they come from the crossed pyramidal tracts of the lateral columns and that none of them are derived from the anterior columns. The fibres of the external portion of the anterior pyramids come from the direct pyramidal tracts of the cord. At the site of the decussation, the pyramids are composed entirely of white matter; but as the fibres spread out to pass to the encephalon above, they present nodules of gray matter between the fasciculi.

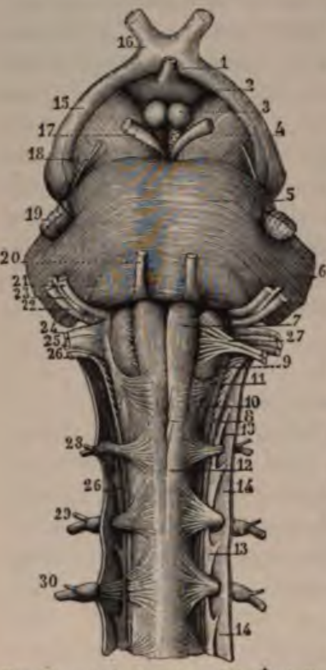


FIG. 231.—*Anterior view of the medulla oblongata* (Sappey).

1, infundibulum; 2, tuber cinereum; 3, corpora albicantia; 4, cerebral peduncle; 5, pons Varolii; 6, origin of the middle peduncle of the cerebellum; 7, *anterior pyramids of the medulla oblongata*; 8, *decussation of the anterior pyramids*; 9, *olivary bodies*; 10, *restiform bodies*; 11, *arciform fibres*; 12, upper extremity of the spinal cord; 13, ligamentum denticulatum; 14, 14, dura mater of the cord; 15, optic tracts; 16, chiasm of the optic nerves; 17, motor oculi communis; 18, patheticus; 19, fifth nerve; 20, motor oculi externus; 21, facial nerve; 22, auditory nerve; 23, nerve of Wrisberg; 24, glosso-pharyngeal nerve; 25, pneumogastric; 26, 26, spinal accessory; 27, sublingual nerve; 28, 29, 30, cervical nerves.

External to the anterior pyramids, are the corpora olivaria. These are oval and are surrounded by a distinct groove. They are white externally and contain a gray nucleus called the corpus dentatum.

External to the corpora olivaria, are the restiform bodies, formed chiefly of white matter and constituting the postero-lateral portion of the medulla. They are continuous with the posterior white columns of the cord. The restiform bodies spread out as they ascend, and pass to the cerebellum, forming a great portion of the inferior peduncles. Some fibres from the restiform bodies pass to the cerebrum.

Beneath the olivary bodies and between the anterior pyramids and the restiform bodies, are the lateral tracts of the medulla, sometimes called the intermediary or lateral fasciculi, or the funiculi of Rolando. These are composed of an intimate mixture of white and gray matter and have a yellowish-gray color. They receive all that portion of the antero-lateral columns of the cord which does not enter into the composition of the anterior pyramids. They are usually described as parts of the restiform bodies, but they are peculiarly important, from the fact that they contain the gray centre presiding over respiration; and for that reason they are here described as distinct fasciculi.

The posterior pyramids (funiculi graciles) are the smallest of all. They pass upward to the cerebellum, without decussating, joining the restiform bodies above. They are composed chiefly of white matter. As they pass upward in the medulla, they diverge, leaving a space at the fourth ventricle.

The fourth ventricle is the cavity between the pons Varolii, the medulla oblongata and cerebellum. It is lozenge-shaped, the acute angles being above and below. The upper angle extends to the upper border of the pons, and the lower angle, to the lower border of the olivary bodies. The triangles which form this lozenge are of nearly equal size. The superior triangle is bounded laterally by the superior peduncles of the cerebellum, as they converge to meet at the corpora quadrigemina. The inferior triangle is bounded laterally by the funiculi graciles and the restiform bodies of the medulla, which diverge at its lower angle. The arched roof of the ventricle is formed by the valve of Vieussens, which is stretched between the superior peduncles of the cerebellum and covers the anterior triangle, and the cerebellum, which covers the posterior triangle. Beneath the cerebellum, is a reflection of the pia mater. The fourth ventricle communicates above with the third ventricle, by the aqueduct of Sylvius, below with the subarachnoid space, by the foramen of Magendie, and by a small opening below with the central canal of the cord. The floor of the ventricle is formed by the posterior surface of the pons above and the medulla below. It presents a fissure in the median line, which terminates below in the calamus scriptorius. By the sides of the median fissure, are the fasciculi teretes, which correspond to the intermediary fasciculi of the medulla. Little eminences in the floor indicate the situation of nuclei of origin of cranial nerves. The floor is composed mainly of a layer of gray matter, continuous with the gray commissure of the cord. The lower portion of the floor is marked by transverse lines of white matter emerging from the median fissure.

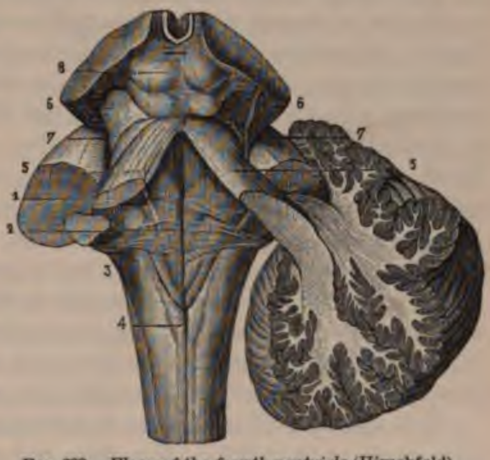



FIG. 232.—*Floor of the fourth ventricle* (Hirschfeld). 1, median fissure, between the fasciculi teretes; 2, transverse, white striæ; 3, inferior peduncle of the cerebellum; 4, posterior pyramid (funiculus gracilis); 5, 5, superior peduncles (divided) of the cerebellum; 6, 6, bands to the side of the crura cerebri; 7, 7, lateral grooves of the crura cerebri; 8, corpora quadrigemina.

The two lateral halves of the posterior portion of the medulla are connected together by fibres arising from the gray matter of the lateral tracts, or intermediary fasciculi, passing obliquely, in a curved direction from behind forward, to the raphe in the median line. There are also fibres passing from before backward, to form a posterior commissure, and fibres arising from the cells of the olivary bodies, which connect the gray substance of the lateral halves. Commissural fibres also connect the gray matter of the lateral tracts with the corpora dentata of the olivary bodies, and the olivary bodies with the cerebellum, their fibres forming part of the inferior peduncles of the cerebellum. In addition it is probable that fibres, taking their origin from all of the gray nodules of the medulla, pass to the parts of the encephalon situated above.

The uncrossed pyramidal tracts of the spinal cord (columns of Türck) pass to the encephalon, by direct fibres situated at the outer border of the anterior pyramids of the medulla.

The crossed pyramidal tracts of the cord decussate in the lower portion of the medulla and constitute the greatest part of the anterior pyramids.

Fibres from the anterior fundamental fasciculi, the anterior radicular zone and from the mixed lateral columns of the cord, probably pass to the gray matter of the medulla.

The direct cerebellar fasciculi of the cord are continuous with the funiculi graciles of the medulla.

The columns of Burdach are continuous with the restiform bodies of the medulla.

The columns of Goll pass to the medulla and are lost in the fasciculi graciles.

As far as the fibres of origin of the cranial nerves are concerned, it may be stated in general terms that a number of the motor roots arise from the gray matter of the floor of the fourth ventricle, the roots of the sensory nerves arising from gray matter in the posterior portions.

## Uses of the Medulla Oblongata.

It is hardly necessary to discuss the action of the medulla oblongata as a conductor of sensory impressions and of motor stimulus to and from the brain. It is evident that there is conduction of this kind from the spinal cord to the ganglia of the encephalon, and this must take place through the medulla; a fact which is inevitable, from its anatomical relations, and which is demonstrated by its section in living animals. Nor is it necessary to dwell upon the general properties of the medulla, in which it resembles the spinal cord, at least as far as has been demonstrated by experiments upon living animals or upon animals just killed. It is difficult to expose this part in the higher classes of animals, but experiments show that it is sensitive on its posterior surface and insensible in front. The difficulty of observing the phenomena which follow its stimulation in living animals has rendered it impossible to determine the limits of its excitability and sensibility as exactly as has been done for the different portions of the cord.

It is also somewhat difficult to determine whether the action of the medulla itself, in its relations to motion and sensation, be crossed or direct. As regards conduction from the brain, the direction is sufficiently well shown by cases of cerebral disease, in which the paralysis, in simple lesions, is on the opposite side of the body.

The action of the medulla as a reflex nerve-centre depends upon its gray matter. When this gray substance is destroyed, certain important reflex phenomena are instantly abolished. From its connection with various of the cranial nerves, one would expect it to play an important part in the movements of the face, in deglutition, in the action of the heart and of various glands etc., important points which are fully considered in their appropriate place. The various reflex centres in the medulla have been located chiefly by a study of the relations of the gray matter to the deep fibres of origin of certain of the cranial nerves. The centre for the orbicularis oculi muscle is related to the origin of the large root of the fifth nerve and the origin of the facial; and the integrity of these two nerves is necessary to the reflex act of closure of the eyelids. The impression which produces the act of sneezing is conveyed to the medulla through the nasal branch of the fifth—possibly sometimes through the olfactory nerves—and excites certain of the expiratory muscles. Impressions conveyed to the medulla by certain sensory branches of the pneumogastrics give rise to the reflex acts of coughing. The reflex acts of swallowing and vomiting also depend upon centres in the medulla oblongata. There are centres, also, which influence the glycogenic action of the liver, the secretion of saliva and the secretion of sweat. The vaso-motor centres will be considered in connection with the physiology of the vaso-motor nerves. The centres connected with respiration are so important that they demand special description.

*Respiratory Nerve-Centre.*—In 1809, Legallois made a number of experiments upon rabbits, cats and other animals, in which he showed that respiration depends upon the medulla oblongata and not upon the brain; and he farther located the part which presides over the respiratory movements, at the site of origin of the pneumogastric nerves. Flourens, in his elaborate experiments upon the nerve-centres, extended the observations of Legallois, and limited the respiratory centre in the rabbit, between the upper border of the roots of the pneumogastrics and a plane situated about a quarter of an inch (6·4 mm.) below the lowest point of origin of these nerves; these limits, of course, varying with the size of the animal. Following these experiments, Longet has shown that the respiratory centre does not occupy the whole of the medulla included between the two planes first indicated by Flourens, but that it is confined to the gray matter of the lateral tracts, or the intermediary fasciculi. This was demonstrated by the fact that respiration persists in animals after division of the anterior pyramids and the restiform bodies. Subsequently, Flourens restricted the limits of the respiratory centre and fully confirmed the observations of Longet.

The portion of the medulla oblongata above indicated presides over the movements of respiration and is the true respiratory nerve-centre. Nearly all who have repeated the experiments of Flourens have found that the spinal cord may be divided below the medulla oblongata, and that all of the encephalic ganglia above may be removed, respiratory movements still persisting. It is a very common thing in vivisections to kill an animal by breaking up the medulla. When this is done there are no struggles and no manifestations of the distress of asphyxia. The respiratory muscles simply cease their action, and the animal loses instantly the sense of want of air. A striking contrast to this is presented when the trachea is tied or when all of the respiratory muscles are paralyzed without touching the medulla.

The relations of the respiratory centre have already been fully considered in connection with the physiology of respiration. Under normal conditions, the centres on the two sides probably operate through the pneumogastric nerves and the respiratory movements on the two sides are synchronous. That there is a respiratory centre on either side, is shown by the experiment of dividing the medulla longitudinally in the median line, the respiratory movements afterward continuing with regularity. If, now, the pneumogastric be divided on one side, the respiratory movements on that side become slower and are no longer synchronous with the movements on the opposite side. This shows that while the respiratory centres on the two sides normally act together, being undoubtedly connected with each other by commissural fibres, each one has independent connections with the pneumogastric on the corresponding side of the body.

*Cardiac Centres.*—There can be scarcely any doubt with regard to the existence of cardiac centres in the medulla—perhaps an inhibitory centre and an acceleratory centre—but the situation of these centres has not been exactly determined. The influence of the nerves and nerve-centres over the movements of the heart has been fully considered in connection with the physiology of the circulation.

*Vital Point* (*so called*).—Since it has been definitely ascertained that destruction of a restricted portion of the gray substance of the medulla produces instantaneous and permanent arrest of the respiratory movements, Flourens and others have called this centre the vital knot, destruction of which is immediately followed by death. With the existing knowledge of the properties and uses of the different tissues and organs of which the body is composed, it is almost unnecessary to present any arguments to show the unphilosophical character of such a proposition. One can hardly imagine such a thing as instantaneous death of the entire organism; and still less can it be assumed that any restricted portion of the nervous system is the one, essential vital point. Probably, a very powerful electric discharge passed through the entire cerebro-spinal axis produces the nearest approach to instantaneous death; but even then it is by no means certain that some parts do not for a time retain their physiological properties. In apparent death, the nerves and the heart may be shown to retain their characteristic properties; the muscles will contract under stimulus, and will appropriate oxygen and give off carbon dioxide, or respire; the glands may be made to secrete, etc.; and no one can assume that under these conditions, the entire organism is dead. There seems to be no such thing as death, except as the various tissues and organs which go to make up the entire body become so altered as to lose their physiological properties beyond the possibility of restoration; and this never occurs for all parts of the organism in an instant. A person drowned may be to all appearances dead, and would certainly die without measures for restoration; yet in such instances, restoration may be accomplished, the period of apparent death being simply a blank, as far as the recollection of the individual is concerned. It is as utterly impossible to determine the exact instant when the vital principle, or whatever it may be called, leaves the body in death, as to indicate the time when the organism becomes a living being. Death is nothing more than a permanent destruction of so-called vital physiological properties; and this occurs successively, and at different times, for different tissues and organs.

When it is seen that frogs will live for weeks, and sometimes for months, after destruction of the medulla oblongata, and that in mammals, by keeping up artificial respiration, many of the most important physiological acts, such as the movements of the heart, may be prolonged for hours after decapitation, one can understand the physiological absurdity of the proposition that there is any such thing as a vital point, in the medulla or in any part of the nervous system.

There is little to be said concerning certain ganglia and other parts of the brain that have not yet been considered. The olfactory ganglia preside over olfaction and will be treated of fully in connection with the special senses. The pineal gland and the pituary body, in their structure, present a certain resemblance to the ductless glands, and their anatomy has been considered in another chapter. Passing over the purely theoretical views of the older writers, who had very indefinite ideas of the action of any of the encephalic ganglia, it can only be said that the uses of the pineal gland and pituitary body in the economy are entirely unknown. The same remark applies to the corpus callosum, the septum lucidum, the ventricles, hippocampi and various other parts that are necessarily described in anatomical works. It is useless to discuss the early or even the recent speculations with regard to the uses of these parts, which are entirely unsupported by experimental or pathological facts and which have not advanced positive knowledge.

### Rolling and Turning Movements following Injury of Certain Parts of the Encephalon.

The remarkable movements of rolling and turning, produced by section or injury of certain of the commissural fibres of the encephalon, are not very important in their bearing upon the uses of the brain, and they are rather to be classed among the curiosities of experimental physiology. These movements follow unilateral lesions and are dependent, to a certain extent, upon a consequent inequality in the power of the muscles on one side, without actual paralysis. Vulpian has enumerated the following parts, injury of which, upon one side, in living animals, may determine movements of rotation:

"1. Cerebral hemispheres;

"2. Corpora striata;

"3. Optic thalami (Flourens, Longet, Schiff);

"4. Cerebral peduncles (Longet);

"5. Pons Varolii;

"6. Tubercula quadrigemina, or bigemina (Flourens);

"7. Peduncles of the cerebellum, especially the middle, and the lateral portions of the cerebellum (Magendie);

"8. Olivary bodies, restiform bodies (Magendie);

"9. External part of the anterior pyramids (Magendie);

"10. Portion of the medulla from which the facial nerve arises (Brown-Séquard);

"11. Optic nerves;

"12. Semicircular canals (Flourens); auditory nerve (Brown-Séquard)."

To the parts above enumerated, Vulpian added the upper part of the cervical portion of the spinal cord.

The movements which follow unilateral injury of the parts mentioned above are of two kinds; viz., rolling of the entire body on its longitudinal axis, and turning, always in one direction, in a small circle, called by the French the movement of *manége*. A capital point to determine in these phenomena is whether the movements be due to paralysis or enfeeblement of certain muscles upon one side of the body, to a direct or reflex irritation of the parts of the nervous system involved or to both of these causes combined. The experiments of Brown-Séquard and others show that the movements may be due to irritation alone, for they occur when parts of the encephalon and the upper portions of the cord are simply pricked, without section of fibres. When there is extensive division of fibres, it is probable that the effects of the enfeeblement of certain muscles are added to the phenomena produced by simple irritation. The most satisfactory explanation of these movements is the one proposed by Brown-Séquard, who attributed them to a more or less convulsive action of muscles on one side of the body, produced by irritation of the nerve-centres. He regarded the rolling as simply an exaggeration of the turning movements, and places both in the same category.

It is not necessary to enter into an extended discussion of the above experiments. In some of them, the movements have been observed toward the side operated upon, and in others, toward the sound side. These differences probably depend upon the fact that in certain experiments, the fibres are involved before their decussation, and in others, after they have crossed in the median line. In some instances, the movements may be due to a reflex action, from stimulation of afferent fibres, and in others, the action of the irritation may be direct. Judging from the fact that most of the encephalic commissural fibres are apparently insensible and inexcitable under direct stimulation, it is probable that the action generally is reflex.

# CHAPTER XX.

## *SYMPATHETIC NERVOUS SYSTEM—SLEEP.*

**General arrangement of the sympathetic system—General properties of the sympathetic ganglia and nerves —Direct experiments on the sympathetic—Vaso-motor centres and nerves—Reflex vaso-motor phenomena—Vaso-inhibitory nerves—Trophic centres and nerves (so-called)—Sleep—Condition of the brain and nervous system during sleep—Anæsthesia and sleep produced by pressure upon the carotid arteries —Differences between natural sleep and stupor or coma—Regeneration of the brain-substance during sleep—Condition of the organism during sleep.**

LIKE the cerebro-spinal system, the sympathetic is composed of centres, or ganglia, and nerves, at least as far as can be seen from its anatomy. The ganglia contain nerve-cells, most of which differ but little from the cells of the encephalon and spinal cord. The nerves are composed of fibres, some of which are nearly identical in structure with the ordinary motor and sensory fibres, while many are the so-called gelatinous fibres. The fibres are connected with the nerve-cells in the ganglia, and the ganglia are connected with each other by commissural fibres. These ganglia constitute a continuous chain on either side of the body, beginning above, by the ophthalmic ganglia, and terminating below in the ganglion impar. It is important to note, however, that the chain of sympathetic ganglia is not independent, but that each ganglion receives motor and sensory filaments from the cerebro-spinal nerves, and that filaments pass from the sympathetic to the cerebro-spinal system. The general distribution of the sympathetic filaments is to mucous membranes—and possibly to integument—to non-striated muscular fibres, and particularly to the muscular coat of the arteries. As far as has been shown by anatomical investigations, there are no fibres derived exclusively from the sympathetic which are distributed to striated muscles, except those which pass to the muscular tissue of the heart. Near the terminal filaments of the sympathetic, in most of the parts to which these fibres are distributed, there exist large numbers of ganglionic cells.

The general arrangement of the sympathetic ganglia and the distribution of the nerves may be stated very briefly; but a knowledge of certain anatomical points is indispensable as an introduction to an intelligent study of the physiology of this system.

In the cranium, are the four cranial ganglia; the ophthalmic, the spheno-palatine, the otic and the submaxillary. In the neck, are the three cervical ganglia; the superior, middle and inferior. In the chest, are the twelve thoracic ganglia, corresponding to the twelve ribs. The great semilunar ganglia, the largest of all and sometimes called the abdominal brain, are in the abdomen, by the side of the cœliac axis. In the lumbar region, in front of the spinal column, are the four lumbar ganglia. In front of the sacrum, are the four or five sacral, or pelvic ganglia; and finally, in front of the coccyx, is a small, single ganglion, the last of the sympathetic chain, called the ganglion impar. Thus, the sympathetic cord, as it is sometimes called, consists of twenty-eight to thirty ganglia on either side, terminating below in a single ganglion.

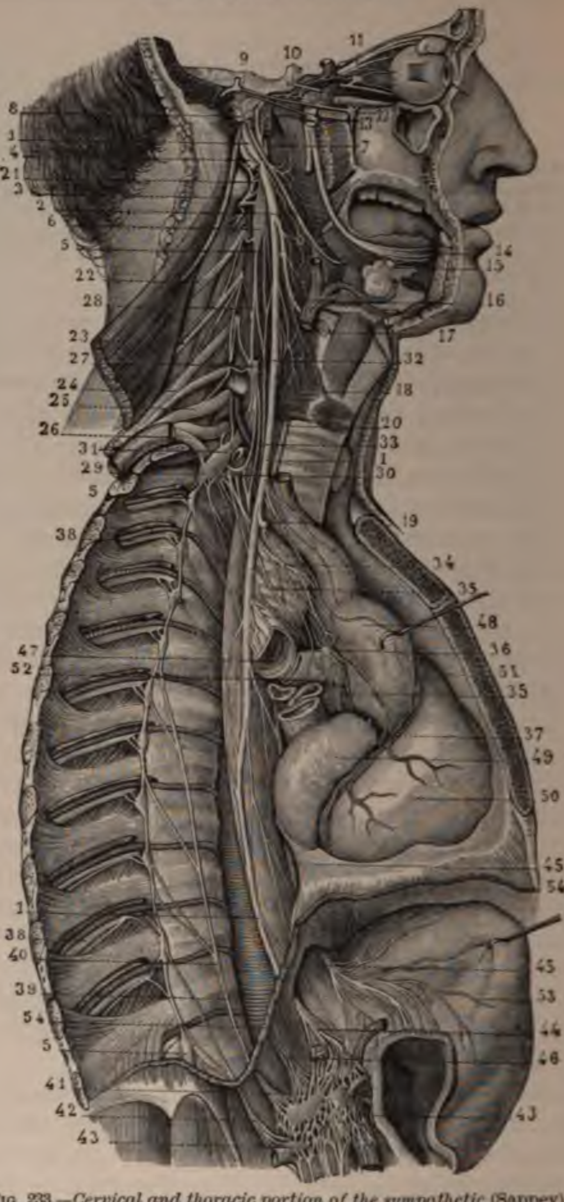



FIG. 233.—*Cervical and thoracic portion of the sympathetic* (Sappey).

1, 1, 1, right pneumogastric ; 2, glosso-pharyngeal ; 3, spinal accessory ; 4, sublingual ; 5, 5, 5, *chain of ganglia of the sympathetic* ; 6, *superior cervical ganglion* ; 7, *branches to the carotid* ; 8, nerve of Jacobson ; 9, *filaments from the facial, to the spheno-palatine and to the otic ganglion* ; 10, motor oculi externus ; 11, *ophthalmic ganglion* ; 12, *spheno-palatine ganglion* ; 13, *otic ganglion* ; 14, lingual branch of the fifth nerve ; 15, *submaxillary ganglion* ; 16, 17, superior laryngeal nerve ; 18, external laryngeal nerve ; 19, 20, recurrent laryngeal nerve ; 21, 22, 23, anterior branches of the upper four cervical nerves ; 24, anterior branches of the fifth and sixth cervical nerves ; 25, 26, anterior branches of the seventh and eighth cervical and the first dorsal nerves ; 27, *middle cervical ganglion* ; 28, *cord connecting the two ganglia* ; 29, *inferior cervical ganglion* ; 30, 31, *filaments connecting this with the middle ganglion* ; 32, *superior cardiac nerve* ; 33, *middle cardiac nerve* ; 34, *inferior cardiac nerve* ; 35, 35, *cardiac plexus* ; 36, *ganglion of the cardiac plexus* ; 37, *nerve following the right coronary artery* ; 38, 38, intercostal nerves ; 39, 40, 41, *great splanchnic nerve* ; 42, *lesser splanchnic nerve* ; 43, 43, *solar plexus* ; 44, left pneumogastric ; 45, right pneumogastric ; 46, phrenic nerve ; 47, right bronchus ; 48, aorta ; 49, right auricle ; 50, right ventricle ; 51, 52, pulmonary artery ; 53, stomach ; 54, diaphragm.

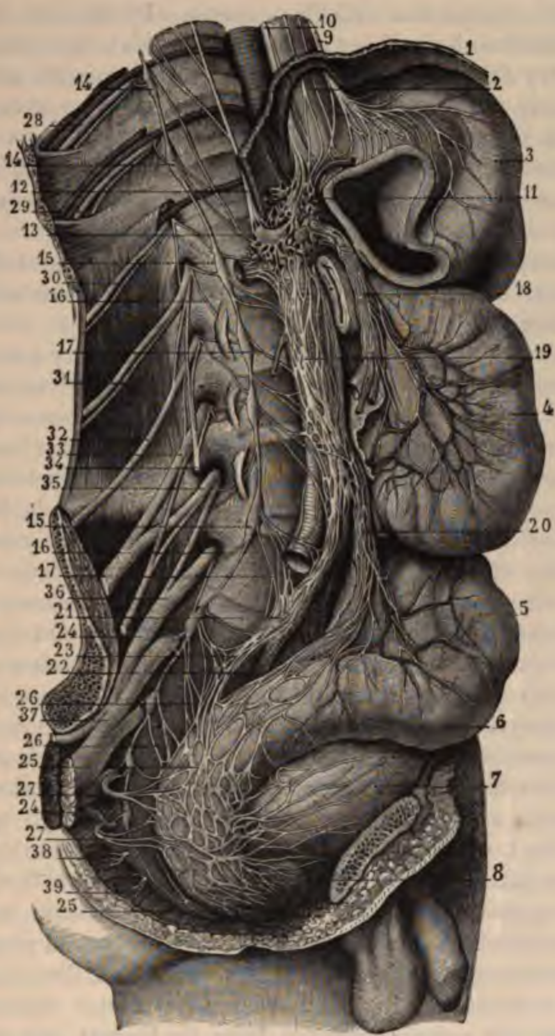



FIG. 234.—*Lumbar and sacral portions of the sympathetic* (Sappey).

1, section of the diaphragm ; 2, lower end of the œsophagus ; 3, left half of the stomach ; 4, small intestine ; 5, sigmoid flexure of the colon ; 6, rectum ; 7, bladder ; 8, prostate ; 9, lower end of the left pneumogastric ; 10, lower end of the right pneumogastric ; 11, *solar plexus* ; 12, *lower end of the great splanchnic nerve* ; 13, *lower end of the lesser splanchnic nerve* ; 14, 14, *last two thoracic ganglia* ; 15, 15, *the four lumbar ganglia* ; 16, 16, 17, 17, *branches from the lumbar ganglia* ; 18, *superior mesenteric plexus* ; 19, 21. 22, 23, *aortic lumbar plexus* ; 20, *inferior mesenteric plexus* ; 24, 24, *sacral portion of the sympathetic* ; 25, 25, 26, 26, 27, 27, *hypogastric plexus* ; 28, 29, 30, tenth, eleventh and twelfth dorsal nerves ; 31, 32, 33, 34, 35, 36, 37, 38, 39, lumbar and sacral nerves.

*Cranial Ganglia.*—The ophthalmic, lenticular, or ciliary ganglion is situated deeply in the orbit, is of a reddish color and about the size of a pin's-head. It receives a motor branch from the third pair and sensory filaments from the nasal branch of the ophthalmic division of the fifth. It is also connected with the cavernous plexus and with Meckel's ganglion. Its so-called motor and sensory roots from the third and the fifth pair have already been described in connection with these nerves. Its filaments of distribution are the ten or twelve short ciliary nerves, which pass to the ciliary muscle and the iris. A very delicate filament from this ganglion passes to the eye, with the central artery of the retina, in the canal in the centre of the optic nerve.

The uses of the ophthalmic ganglion are related mainly to the action of the ciliary muscle and iris; and it is only necessary here to indicate its anatomical relations, leaving its physiology to be taken up in connection with the physiology of the sense of sight.

The spheno-palatine, or Meckel's ganglion, is the largest of the cranial ganglia. It is triangular in shape, reddish in color, and is situated in the spheno-maxillary fossa, near the spheno-palatine foramen. It receives a motor root from the facial, by the Vidian nerve. Its sensory roots are the two spheno-palatine branches from the superior maxillary division of the fifth. It has a large number of branches of distribution. Two or three delicate filaments enter the orbit and go to its periosteum. Its other branches, which it is unnecessary to describe fully in detail, are distributed to the gums, the membrane covering the hard palate, the soft palate, the uvula, the roof of the mouth, the tonsils, the mucous membrane of the nose, the middle auditory meatus, a portion of the pharyngeal mucous membrane, and the levator palati and azygos uvulæ muscles. It is probable that the filaments sent to these two striated muscles are derived from the facial nerve and do not properly belong to the sympathetic system. The ganglion also sends a short branch, of a reddish-gray color, to the carotid plexus.

The otic ganglion, sometimes called Arnold's ganglion, is a small, oval, reddish-gray mass, situated just below the foramen ovale. It receives a motor filament from the facial and sensory filaments from branches of the fifth and the glosso-pharyngeal. Its filaments of distribution go to the mucous membrane of the tympanic cavity and Eustachian tube and to the tensor tympani and tensor palati muscles. Reasoning from the general mode of distribution of the sympathetic filaments, those going to the striated muscles are derived from the facial. It also sends branches to the carotid plexus.

The submaxillary ganglion, situated on the submaxillary gland, is small, rounded, and reddish-gray in color. It receives motor filaments from the chorda tympani and sensory filaments from the lingual branch of the fifth. Its filaments of distribution go to Wharton's duct, to the mucous membrane of the mouth and to the submaxillary gland.

*Cervical Ganglia.*—The three cervical ganglia are situated opposite the third, fifth and seventh cervical vertebræ respectively. The middle ganglion is sometimes wanting, and the inferior ganglion is occasionally fused with the first thoracic ganglion. These ganglia are connected together by the so-called sympathetic cord. They have a number of filaments of communication above, with the cranial and the cervical nerves of the cerebro-spinal system. Branches from the superior ganglion go to the internal carotid, to form the carotid and the cavernous plexus, following the vessels as they branch to their distribution. Branches from this ganglion pass to the cranial ganglia. There are also branches which unite with filaments from the pneumogastric and the glosso-pharyngeal to form the pharyngeal plexus, and branches which form a plexus on the external carotid, the vertebral and the thyroid arteries, following the ramifications of these vessels.

From the cervical portion of the sympathetic the three cardiac nerves arise and pass to the heart, entering into the formation of the cardiac plexus. The superior cardiac nerve arises from the superior ganglion; the middle nerve, the largest of the three, arises from the middle ganglion or from the sympathetic cord, when this ganglion is wanting; and the inferior nerve arises from the inferior cervical ganglion or the first thoracic. These nerves present frequent communications with various of the adjacent cerebro-spinal nerves, penetrate the thorax, and form the deep and superficial cardiac plexuses and the posterior and the anterior coronary plexuses. In these various plexuses, there are found ganglioform enlargements; and upon the surface and in the substance of the heart, are collections of nerve-cells connected with the fibres.

*Thoracic Ganglia.*—The thoracic ganglia are situated in the chest, beneath the pleura, and rest on the heads of the ribs. They are usually twelve in number, but occasionally two are fused into one. They are connected together by the sympathetic cord. They each communicate by two filaments with the cerebro-spinal nerves. One of these is white, like the spinal nerves, and probably passes to the sympathetic, and the other, of a grayish color, is thought to contain the true sympathetic filaments. From the upper six ganglia filaments pass to the aorta and its branches. The branches which form the posterior pulmonary plexus arise from the third and fourth ganglia. The great splanchnic nerve arises mainly from the seventh, eighth and ninth ganglia, receiving a few filaments from the upper six ganglia. This is a large, white, rounded cord, which penetrates the diaphragm and passes to the semilunar ganglion, sending a few filaments to the renal plexus and the suprarenal capsules. The lesser splanchnic nerve arises from the tenth and eleventh ganglia, passes into the abdomen and joins the cœliac plexus. The renal splanchnic nerve arises from the last thoracic ganglion and passes to the renal plexus. The three splanchnic nerves present frequent anastomoses with each other.

*Ganglia in the Abdominal and the Pelvic Cavity.*—The semilunar ganglia on the two sides send off radiating branches to form the solar plexus. They are situated by the side of the cœliac axis and near the suprarenal capsules. These are the largest of the sympathetic ganglia. From these arise plexuses distributed to various parts in the abdomen, as follows: The phrenic plexus follows the phrenic artery and its branches to the diaphragm. The cœliac plexus subdivides into the gastric, hepatic and splenic plexuses, which are distributed to organs, as their names indicate. From the solar plexus different plexuses are given off, which pass to the kidneys, the suprarenal capsules, the testes in the male and the ovaries in the female, the intestines (by the superior and inferior mesenteric plexuses), the upper part of the rectum, the abdominal aorta and the vena cava. The filaments follow the distribution of the blood-vessels in the solid viscera.

The lumbar ganglia, four in number, are situated in the lumbar region, upon the bodies of the vertebræ. They are connected with the ganglia above and below and with each other by the sympathetic cord, receiving, like the other ganglia, filaments from the spinal nerves. Their branches of distribution form the aortic lumbar plexus and the hypogastric plexus and follow the course of the blood-vessels.

The four or five sacral ganglia and the ganglion impar are situated by the inner side of the sacral foramina and in front of the coccyx. These are connected with the ganglia above and with each other, and they receive filaments from the sacral nerves, there being generally two branches of communication for each ganglion. The filaments of distribution go to all of the pelvic viscera and blood-vessels. The inferior hypogastric, or pelvic plexus is a continuation of the hypogastric plexus above, and receives a few filaments from the sacral ganglia. The uterine nerves go to the uterus and the Fallopian tubes. In the substance of the uterus the nerves are connected with small collections of ganglionic cells. The sympathetic filaments are prolonged into the upper and lower extremities, following the course of the blood-vessels and terminating in their muscular coat.

The filaments of the sympathetic, at or near their terminations, are connected with ganglionic cells, not only in the heart and the uterus, but in the blood-vessels, lymphatics, the coccygeal gland, the submucous and the muscular layer of the entire alimentary canal, the salivary glands, pancreas, excretory ducts of the liver and pancreas, the larynx, trachea, pulmonary tissue, bladder, ureters, the entire generative apparatus, suprarenal capsules, thymus, lachrymal canals, ciliary muscle and the iris. In these situations nerve-cells have been demonstrated by various observers, and it is probable that they exist everywhere in connection with the terminal filaments of this system of nerves.

*General Properties of the Sympathetic Ganglia and Nerves.*—The sympathetic ganglia and nerves possess a dull sensibility, which is particularly marked in the ganglia. That the nerves contain afferent fibres, is shown by certain reflex phenomena.

Stimulation of the sympathetic produces muscular movements, but these are confined generally to non-striated muscular fibres, to which these nerves are largely distributed. The muscular movements do not immediately follow stimulation of the nerves, but there is a long, latent period. The muscular contraction, also, persists for a time and the subsequent relaxation is slow. The induced current applied to the splanchnic nerves does not produce movements of the intestines, but these movements are excited by the constant current (Legros and Onimus). The properties of the vaso-motor nerves will be considered separately.

The sympathetic ganglia are connected with the motor and sensory divisions of the cerebro-spinal system. Some of the ganglia and nerve-plexuses are directly dependent for their action upon the cerebro-spinal system, while others are capable, at least for a time, of independent action. Among the latter, are the ganglia of the heart, the intestinal plexuses, the plexuses of the uterus and Fallopian tubes, of the ureters and of the blood-vessels.

*Direct Experiments on the Sympathetic.*—The experiments of Pourfour du Petit (1712–1725) were the first to give any positive information regarding the action of the sympathetic system; and these observations may be taken as the starting-point of a definite knowledge of the physiology of the sympathetic, although they showed only the influence of the cervical portion upon the eye. In 1816, Dupuy removed the superior cervical ganglia in horses, with the effect of producing injection of the conjunctiva, increase of temperature in the ear and an abundant secretion of sweat upon one side of the head and neck. These experiments showed that the sympathetic has an important influence upon nutrition, calorification and secretion. In 1851, Bernard divided the sympathetic in the neck on one side in rabbits, and noted on the corresponding side of the head and the ear, increased vascularity and an elevation in temperature of 7° to 11° Fahr. (4° to 6° C.). This condition of increased heat and vascularity continues for several months after division of the nerve. In 1852, Brown-Séquard repeated these experiments and attributed the elevation of temperature directly to an increase in the supply of blood to the parts affected. He made an important advance in the history of the sympathetic, by demonstrating that its section paralyzed the muscular coat of the arteries, and farther, that Faradization of the nerve in the neck caused the vessels to contract. This was the discovery of the vaso-motor nerves, and it belongs without question to Brown-Séquard, who published his observations in August, 1852. A few months later in the same year, Bernard made analogous experiments and presented the same explanation of the phenomena observed.

The important points developed by the first experiments of Bernard and of Brown-Séquard were that the sympathetic system influences the general process of nutrition, and that many of its filaments are distributed to the muscular coat of the blood-vessels. Before these experiments, it had been shown that filaments from this system influenced the contractions of the muscular coats of the alimentary canal.

When the sympathetic is divided in the neck, the local increase in temperature is always attended with a very great increase in the supply of blood to the side of the head corresponding to the section. The increased temperature is due to a local exaggeration of the nutritive processes, apparently dependent directly upon the hyperæmia. There are many instances in pathology, of local increase in temperature attending increased supply of blood to restricted parts. In an experiment by Bidder, after excising about half an inch (12·7 mm.) of the cervical sympathetic in a half-grown rabbit, the ear on that side, in the course of about two weeks, became distinctly longer and broader than the other.

It is easy to observe the effects of dividing the sympathetic in the neck, but analogous phenomena have been noted in other parts. Among the most striking of these experiments are those reported by Samuel, who described an intense hyperæmia of the mucous membrane of the stomach and intestines, following extirpation of the cœliac plexus. By comparative experiments it was shown that this did not result from the peritonitis produced by the operation.

As regards secretion, the influence of the sympathetic is very marked. When the sympathetic filaments distributed to a gland are divided, the supply of blood is much increased and an abundant flow of the secretion follows (Bernard). Peyrani has shown that the sympathetic has an influence upon the secretion of urine. When the nerves in the neck are stimulated, the quantity of urine and of urea is increased, and this increase is greater with the induced than with the constant current. When the sympathetic is divided, the quantity of urine and of urea sinks to the minimum.

Moreau published in 1870 a series of observations on the influence of the sympathetic nerves upon the secretion of liquid by the intestinal canal, which are important as affording a possible explanation of the sudden occurrence of watery diarrhœa. In these experiments, the abdomen was opened in a fasting animal, and three loops of intestine, each loop four to eight inches (100 to 200 mm.) long, were isolated by ligatures. All of the nerves passing to the middle loop were divided, taking care to avoid the blood-vessels. The intestine was then replaced, and the wound in the abdomen was closed with sutures. The next day the animal was killed. The two loops with the nerves intact were found empty, as is normal in fasting animals, and the mucous membrane was dry; but the loop with the nerves divided was found filled with a clear, alkaline liquid, colorless or slightly opaline, which precipitated a few flocculi of organic matter on boiling.

*Vaso-Motor Centres and Nerves.*—The principal or dominating vaso-motor centres are situated in the medulla oblongata, one on either side, about one-tenth of an inch (2·5 mm.) from the median line. Each centre, in the rabbit, is about one-eighth of an inch (3 mm.) long and about one-sixteenth of an inch (1·5 mm.) wide. Its lower border is about one-fifth of an inch (5 mm.) above the calamus scriptorius. Each side of the body has its special vaso-motor centre, and very few if any of the vaso-motor fibres decussate. The situation of the vaso-motor centres in the medulla has been determined by successive removal of the nerve-centres above. If the central end of a large cerebro-spinal nerve be stimulated in an animal poisoned with curare, the vaso-motor nerves produce contraction of the blood-vessels, by reflex action, and there is a rise in the blood-pressure. The action is not interfered with by removal of the encephalic ganglia from above downward, until the part of the medulla containing the vaso-motor centres is reached. When these centres are removed, the reflex vaso-motor action is permanently arrested.

Subordinate vaso-motor centres exist in the spinal cord. When the vaso-motor centre in the medulla is destroyed, there is a fall in the blood-pressure; but if the circulation be continued, after a time the blood-vessels regain their "tone" and the pressure may then be affected by reflex action. It is probable that these spinal centres exist throughout the dorsal region and in the upper part of the lumbar region of the cord.

All the vaso-motor nerves are derived from the medulla oblongata and the spinal cord. Some of the vaso-motor fibres to the head pass in the trunks of the motor cranial nerves, but most of them come from the anterior roots of some of the spinal nerves and pass to the head by the filaments of distributiôn of the cervical sympathetic. The vaso-motor fibres pass in the lateral columns of the cord, and from the cord, in the anterior roots of the spinal nerves, in the dog, as far down as the second pair of lumbar nerves. These fibres are medullated but are of small size. They pass to the blood-vessels either through branches from the sympathetic ganglia or through the ordinary cerebro-spinal nerves. They are therefore not confined to branches of the sympathetic, as Bernard has shown by the following experiment: He divided the fourth, fifth, sixth, seventh and eighth pairs of lumbar nerves on one side in a dog, at the spinal column, and paralyzed motion and sensation in the leg of that side, but the temperature of the two sides remained the same. He afterward exposed and divided the sciatic nerve on that side, and then noted decided increase in temperature. This experiment, which is only one of a large number, shows that the ordinary mixed nerves contain vaso-motor fibres, which are entirely independent of the nerves of motion and sensation, a fact which is now well known to physiologists and has frequently been illustrated in cases of disease in the human subject.

The vaso-motor nerves are capable of influencing local circulations, probably through distinct centres for different parts. Direct stimulation of the principal vaso-motor centre (10 to 12 or more single induction shocks per second for strong currents or 20 to 25 for moderate currents) increases the blood-pressure to the maximum.

The contractile coats of the veins and lymphatics probably are influenced by vaso-motor nerves, but there is little known of the mechanism of this action.

*Reflex Vaso-Motor Phenomena.*—The most important physiological acts connected with the vaso-motor nerves are reflex. It is evident from experiments on the inferior animals and observations on the human subject that there are afferent as well as efferent nerves. The reflex acts connected with secretion have already been considered; but there are other phenomena that demand a brief description.

As regards animal heat, the phenomena of which are intimately connected with the supply of blood to the parts, it is important to note the observations of Brown-Séquard and Lombard, who found that pinching of the skin on one side was attended with a diminution in the temperature in the corresponding member of the opposite side, and that sometimes, when the irritation was applied to the upper extremities, changes were produced in the temperature of the lower limbs. Tholozan and Brown-Séquard found, also, that lowering the temperature of one hand produced a considerable depression in the heat of the other hand, without any notable diminution in the general heat of the body. Brown-Séquard showed that by immersing one foot in water at 41° Fahr. (5° C.) the temperature of the other foot was diminished by about 7° Fahr. (4° C.) in the course of eight minutes.

These experiments show that certain impressions made upon the sensory nerves affect the animal heat, by reflex action. As section of the sympathetic filaments increases the heat in particular parts, with an increase in the supply of blood, and their Faradization reduces the quantity of blood and diminishes the temperature, it is reasonable to infer that the reflex action takes place through the vaso-motor nerves. If it be assumed that the impression is conveyed to the centres by the nerves of general sensibility, and that the vessels are modified in their caliber and the heat is affected through the sympathetic fibres, it remains only to determine the situation of the centres which receive the impression and generate the stimulus. These centres are situated in the cerebro-spinal axis.

The existence of vaso-motor nerves and their connection with centres in the cerebro-spinal axis are now sufficiently well established. It is certain, also, that centres presiding over particular acts may be distinctly located, as the genito-spinal centre, in the spinal cord opposite the fourth lumbar vertebra, and the cilio-spinal centre, in the cervical region of the cord. An impulse generated in these centres, sometimes as the result of impressions received through the nerves of general sensibility, produces contraction of the non-striated muscular fibres of the iris, vasa deferentia etc., including the muscular walls of the blood-vessels. The contraction of the muscular walls of the vessels is tonic; and when their nerves are divided, relaxation takes place and the vessels are dilated by the pressure of blood. By this action the local circulations are regulated in accordance with impressions made upon sensory nerves, the physiological requirements of certain parts, mental emotions etc. Secretion, the peristaltic movements of the alimentary canal, the movements of the iris etc., are influenced in this way. This action is also illustrated in cases of reflex paralysis, in inflammations as the result of "taking cold," and in many other pathological conditions.

It remains only to show that the phenomena following section of the sympathetic in animals are illustrated in certain cases of disease or injury in the human subject. It is rare to observe traumatic injury confined to the sympathetic in the neck. A single case, however, apparently of this kind, has been reported by Mitchell. A man received a gunshot-wound in the neck. Among the phenomena observed a few weeks after, were contraction of the pupil on the side of the injury, and after exercise, flushing of the face upon that side. There was no difference in the temperature upon the two sides during repose, but no thermometric observations were made when half of the face was flushed by exercise. Bartholow has reported several cases of unilateral sweating of the head (two observed by himself), in several of which there probably was compression of the sympathetic, from aneurism. In those cases in which the condition of the eye was observed, the pupil was found contracted in some and dilated in others. In none of these cases were there any accurate thermometric observations. In a series of observations by Wagner, upon the head of a woman, eighteen minutes after decapitation, powerful stimulation of the sympathetic produced great enlargement of the pupil. In such a case as this, it would not be possible to make any observations on the influence of the sympathetic upon the temperature.

*Vaso-Inhibitory Nerves.*—There are certain nerves, the direct action of which under Faradic stimulation is to dilate certain blood-vessels. These nerves may also be excited by reflex action through the sensory nerves. In many nerves, as the chorda tympani, the nervi erigentes etc., the existence of inhibitory fibres has been demonstrated (Dastre and Morat, Eckhard, Laffont, Vulpian and others). For example, division of the nervi erigentes has no immediate effect on the penis, but Faradization of the peripheral ends of the nerves dilates the blood-vessels and produces erection. Fibres possessing this property undoubtedly exist throughout the body, in the sympathetic and in the motor and mixed nerves; and it is possible that there are vaso-motor inhibitory centres, although such centres have not been located. The mode of action of these nerves is analogous to that of the inhibitory nerve of the heart, restraining and regulating the action of the vaso-motor nerves and allowing the pressure of blood to dilate the vessels. It does not, however seem proper to call them "vaso-dilator" nerves, any more than it would be correct to call the inhibitory nerve of the heart the cardiac dilator nerve.

*Trophic Centres and Nerves (so-called).*—Collections of nerve-cells act as centres presiding over the nutrition of the nerve-fibres with which they are connected; but it has been found that the nutrition of certain parts may be profoundly affected through the nervous system. Many pathologists, relying upon the presence of certain lesions of cells in the cord, in connection with cases of progressive muscular atrophy, admit the existence of trophic cells and nerves. These views, however, rest almost entirely upon pathological observations. Direct experiments upon the sympathetic in animals do not positively show any influence upon nutrition, except as this system of nerves affects the supply of blood to the parts. When a sympathetic nerve is divided, there is an apparent exaggeration of the nutritive processes in particular parts, and there may be inflammatory phenomena, but atrophy of muscles is not observed. Atrophy of muscles, indeed, follows division of cerebro-spinal nerves only, or as cases of disease have shown, disorganization of cells belonging to what are recognized as motor centres. As regards the latter condition, there can be no doubt of the fact that progressive muscular atrophy is attended with disorganization of certain of the motor cells of the spinal cord.

Without fully discussing this subject, which belongs to pathology, the facts may be briefly stated as follows: There may be progressive atrophy of certain muscles, uncomplicated with paralysis except in so far as there is weakness of these muscles due to partial and progressive destruction of their contractile elements. The only constant pathological condition in these cases, aside from the changes in the muscular tissue, is destruction of certain cells in the antero-lateral portions of the cord, with more or less atrophy of the corresponding anterior roots of the nerves. It has never been assumed that there are cells in the cord, presenting anatomical peculiarities by which they may be distinguished from the ordinary motor or sensory elements; but the fact of the degeneration of certain cells, others remaining normal, has led to the distinction by certain writers, of trophic cells, and, of course, these must be connected with the parts by trophic nerves.

There can be no doubt of the fact that the cells of the antero-lateral columns of the spinal cord are connected with motion, and that impulses generated in these cells are conveyed to the muscles by the anterior roots of the spinal nerves. It also is a fact, no less definite, that when a muscle or a part of a muscle is for a long time deprived of the motor influence by which it is brought into action, its fibres undergo atrophy, become altered in structure and lose their contractility. Starting with these two propositions, and assuming that certain of the ordinary motor cells of the cord are destroyed, it is easy to predict the phenomena to be expected as a consequence of such a lesion.

The destruction of certain motor nerve-cells connected with the anterior roots of the spinal nerves would certainly produce degeneration of the nerve-fibres to which they give origin. This occurs when any motor nerves are separated from their cells of origin, and it involves no necessity of assuming the existence of special trophic cells or nerves.

If a few of the motor cells be affected with disease, and if the degeneration be gradual and progressive, there would necessarily be progressive and partial paralysis of the muscles to which their nerves are distributed. This paralysis, confined to a limited number of fibres of particular muscles or sets of muscles, would give the idea of progressive weakening of the muscles, and the phenomena would not be those observed in complete paralysis produced by section of the motor nerves. These are the phenomena observed in progressive muscular atrophy, preceding the paralysis which is the final result of the disease; and these do not of necessity involve the action of any special centres or nerves.

As regards the muscular atrophy itself, if the nervous stimulus be gradually destroyed, the muscular tissue will necessarily undergo progressive degeneration and atrophy.

With the above considerations, the question of the trophic cells and nerves may be left to the pathologist; and the existence of centres and nerves specially and directly influencing the nutrition of the muscular system can be admitted only when it has been demonstrated that there are lesions of particular structures in the nervous system, which produce phenomena that can not be explained by the action of ordinary motor and sensory nerves and of the vaso-motor system. In thus dismissing the question, however, it is not intended to assume that the existence of trophic centres and nerves is impossible. There are certain peculiar changes in tissue in progressive muscular atrophy, and section of nerves produces degenerations of glandular and other structures that are not muscular. Future observations may show that there are special parts of the nervous system presiding over nutrition; but at present, such parts have not been accurately described and isolated, either anatomically or physiologically.

## Sleep.

When it is remembered that about one-third of each day is passed in sleep, and that at this time, voluntary motion, sensation, the special senses and various of the functions of the organism are greatly modified, the importance of a physiological study of this condition is sufficiently apparent. The subject of sleep is most appropriately considered in connection with the nervous system, for the reason that the most important modifications in function are observed in the cerebro-spinal axis and nerves. Repose is as necessary to the nutrition of the muscular system as proper exercise; but repose of the muscles relieves the fatigue due to exercise, without sleep. It is true that after violent and prolonged exertion, there is frequently a desire for sleep, but simple repose will often restore the muscular power. After the most violent effort, a renewal of muscular vigor is most easily and completely effected by rest without sleep, a fact familiar to all who are accustomed to athletic exercises. After prolonged and severe mental exertion, however, or after long-continued muscular effort which involves an excessive expenditure of the so-called nerve-force, sleep becomes an imperative necessity. If the nervous system be not abnormally excited by effort, sleep follows moderate exertion as a natural consequence, and it is the only physiological means of complete restoration; but the two most important muscular acts, viz., those concerned in circulation and respiration, are never completely arrested, sleeping or waking, although they undergo certain modifications.

In infancy and youth, when the organism is in process of development, sleep is more important than in adult life or old age. The infant does little but sleep, eat and digest. In adult life, under perfectly physiological conditions, a person requires about eight hours of sleep; some need less, but few require more. In old age, unless after extraordinary exertion, less sleep is required than in adult life. Each individual learns by experience how much sleep is necessary for perfect health; and there is nothing which more completely incapacitates one for mental or muscular effort, especially the former, than loss of natural rest.

Sleeplessness is one of the most important of the predisposing causes of certain forms of brain-disease, a fact which is well recognized by practical physicians. One of the most severe methods of torture is long-continued deprivation of sleep; and persons have been known to sleep when subjected to acutely painful impressions. Severe muscular effort, even, may be continued during sleep. In forced marches, regiments have been known to sleep while walking; men have slept soundly in the saddle; persons will sometimes sleep during the din of battle; and other instances illustrating the imperative demand for sleep after prolonged vigilance might be cited. It is remarkable, also, how noises to which one has become accustomed may fail to disturb natural rest. Those who have been long habituated to the noise of a crowded city frequently find difficulty in sleeping in the stillness of the country. Prolonged exposure to intense cold induces excessive somnolence, and if this be not resisted, the sleep passes into stupor, the power of resistance to cold becomes rapidly diminished, and death is the result. Intense heat often produces drowsiness, but, as is well known, is not favorable to natural sleep.

Sleep is preceded by a feeling of drowsiness, an indisposition to mental or physical exertion, and a general relaxation of the muscular system. It then requires a decided effort to keep awake. In sleep the voluntary muscles are inactive, the lids are closed, the ordinary impressions of sound are not appreciated, and sometimes there is a dreamless condition, in which all knowledge of existence is lost.

There may be, during sleep, mental operations of which there is no consciousness or recollection, unconscious cerebration, as it was called by Carpenter. It is well known that dreams are vividly remembered immediately on awakening, but that the recollection of them rapidly fades away, unless they be brought to mind by an effort to recall and relate them. Whatever be the condition of the mind in sleep, if the sleep be normal, there is repose of the cerebro-spinal system and an absence of voluntary effort, which restore the capacity for mental and physical exertion.

The impressionability and the activity of the human mind are so great, most of the animal functions are so subordinate to its influence, and the organism is so subject to unusual mental conditions, that it is difficult to determine with exactness the phenomena of sleep that are absolutely physiological and to separate those that are slightly abnormal. It can not be assumed, for example, that a dreamless sleep, in which existence, is as it were a blank, is the only normal condition of repose of the system; nor is it possible to determine what dreams are due to previous trains of thought, to impressions from the external world received during sleep, and are purely physiological, and what are due to abnormal nervous influences, disordered digestion, etc. It may be assumed, however, that an entirely refreshing sleep is normal.

That reflex ideas originate during sleep, as the result of external impressions, there can be no doubt; and many remarkable experiments upon the production of dreams of a definite character, by subjecting a person during sleep to peculiar influences, have been recorded. The hallucinations produced in this way are called hypnagogic, and they occur usually when the subject is not in a condition favorable to sound sleep.

As regards dreams due to external impressions, it is a curious fact, which has been noted by many observers and is one which accords with the personal experience of all who have reflected upon the subject, that trains of thought and imaginary events, which seem to pass over a long period of time in dreams, actually occur in the brain within a few seconds. A person is awakened by a certain impression, which undoubtedly has given rise to a dream that seemed to occupy hours or days, and yet the period of time between the impression and the awakening was hardly more than a few seconds; and persons will drop asleep for a very few minutes, and yet have dreams with the most elaborate details and apparently of great length. It is unnecessary to cite the accounts of literary compositions of merit, the working out of difficult mathematical problems in dreams, etc., some of which are undoubtedly accurate. If it be true that the mind is capable of forming consecutive ideas during sleep—which can hardly be doubted—there is no good reason why these phenomena should not occur and the thoughts should not be remembered and noted immediately on awakening. In most dreams, however, the mind is hardly in a normal condition, and the brain generally loses the power of concentration and of accurate reasoning.

*Condition of the Brain and Nervous System during Sleep.*—During sleep the brain may be in a condition of absolute repose—at least, as far as there is any subjective knowledge of mental operations—or there may be more or less connected trains of thought. There is, also, as a rule, absence of voluntary effort, although movements may be made to relieve discomfort from position or external irritation, without awakening. The sensory nerves retain their properties, although the general sensibility is somewhat blunted; and the same may be said of the special senses of hearing, smell, and probably of taste. There is every reason to believe that the action of the sympathetic system is not disturbed or affected by sleep, if the influence of the vaso-motor nerves upon the circulation in the brain be excepted.

Two opposite theories have long been in vogue with regard to the immediate cause of sleep. In one, this condition is attributed to venous congestion and increased pressure of blood in the brain, and this view probably had its origin in the fact that cerebral congestion induces stupor or coma. Stupor and coma, however, are entirely distinct from natural sleep; for in the former the action of the brain is entirely suspended, there is no consciousness, no dreaming, and the condition is manifestly abnormal. In animals rendered comatose by opium, the brain when exposed is found deeply congested with venous blood. The same condition often obtains in profound anæsthesia by chloroform, but a state of the brain very nearly resembling normal sleep is observed in anæsthesia by ether. These facts have been demonstrated by experiments upon living animals, and have been observed in the human subject in cases of injury of the head. When opium is administered in large doses, the brain is congested during the condition of stupor or coma, but this congestion is relieved when the animal passes, as sometimes happens, from the effects of the agent into a natural sleep. In view of these facts and others which will be stated hereafter, it is unnecessary to discuss the theory that sleep is attended with or is produced by congestion of the cerebral vessels.

The idea that the circulation in the brain is diminished during sleep has long been entertained by some physiologists; but until within a few years, it has rested chiefly upon theoretical considerations. The experiments of Durham (1860) seem to demonstrate that the supply of blood to the brain is always greatly diminished during sleep. These experiments were made upon dogs. A piece of the skull was removed with a trephine, and a watch-glass was accurately fitted to the opening and cemented at the edges with Canada balsam. When the animals operated upon were awake, the vessels of the pia mater were seen moderately distended and the circulation was active; but during perfectly natural sleep, the brain retracted and became pale. "The contrast between the appearance of the brain during its period of functional activity and during its state of repose or sleep was most remarkable." There can be hardly any doubt, after these experiments, that the cerebral circulation is considerably diminished in activity during sleep.

The influence of diminished supply of blood to the brain has been illustrated by compression of both carotid arteries. In an experiment performed upon his own person, Fleming produced immediate and profound sleep in this way, and this result invariably followed in subsequent trials upon himself and others. Waller produced anæsthesia in patients by pressure upon both pneumogastric nerves; but the nerves are so near the carotid arteries that they could hardly be compressed, in the human subject, without interfering with the current of blood, and such experiments do not positively show whether the loss of sensibility be due to pressure upon the nerves or upon the vessels. In some rare instances in which both carotid arteries have been tied in the human subject, it has been stated that there is an unusual drowsiness following the necessary diminution in the activity of the cerebral circulation; but this result is by no means constant, and the morbid conditions involving so serious an operation are usually such as to interfere with their value as facts bearing upon the question under consideration. As far as the human subject is concerned, the most important facts are the results of compression of both carotids in healthy persons. These, as well as experiments on animals, all go to show that the supply of blood to the brain is diminished during natural sleep, and that sleep may be induced by retarding the cerebral circulation by compressing the vessels of supply. When the circulation is interfered with by compressing the veins, congestion is the result, and there is stupor or coma.

If diminished flow of blood through the cerebral vessels be the cause of natural sleep, it becomes important to inquire how this condition of physiological anæmia is brought about. It must be that when the system requires sleep, the vessels of the brain contract in obedience to a stimulus received through the sympathetic system of nerves, diminishing the supply of blood, here, as in other parts under varied physiological conditions. The vessels of the brain are provided with vaso-motor nerves, and it is sufficient to have noted that the arteries are contracted during sleep, the mechanism of this action being well established by observations upon other parts of the circulatory system.

Little is known of the intimate nature of the processes of nutrition of the brain during its activity and in repose; but there can be no doubt of the fact that there is more or less cerebral action at all times when one is awake. Although the mental processes are much less active during sleep, even at this time, the operations of the brain are not always suspended. It is equally well established that exercise of the brain is attended with physiological wear of nervous tissue, and like other parts of the organism, its tissue requires periodic repose for regeneration of the substance consumed. Analogies to this are to be found in parts that are more easily subjected to direct observation. The muscles require repose after exertion, and the glands, when not actively engaged in discharging their secretions, present intervals of rest. As regards the glands, during the intervals of repose the supply of blood to their tissue is much diminished. It is probable, also, that the muscles in action receive more blood than during rest; but it is mainly when these parts are not active, and when the supply of blood is smallest, that the processes of regeneration of tissue seem to be most efficient. As a rule the activity of parts, while it is attended with an increased supply of blood, is a condition more or less opposed to the processes of repair, the hyperæmia being, apparently, a necessity for the marked and powerful manifestations of their peculiar action. When the parts are active, the blood seems to be required to keep at the proper standard the so-called irritability of the tissues and to increase their power of action under proper stimulus. Exercise increases the power of regeneration and favors full development in the repose which follows; but during rest, the tissues have time to appropriate new matter, and this does not seem to involve a large supply of blood. A muscle is exhausted by prolonged exertion; and the large quantity of blood passing through the tissue carries away carbon dioxide and other products of disassimilation, which are increased in quantity, until it gradually uses up its capacity for work. Then follows repose; the supply of blood is reduced, but under normal conditions, the tissue repairs the waste which has been excited by action, the blood furnishing nutritive matter and carrying away a comparatively small quantity of effete products.

It may safely be assumed that processes analogous to those just described take place in the brain. By absence of voluntary effort, the muscles have time for rest and for the repair of physiological waste, and their action is for the time suspended. As the activity of the brain involves consciousness, volition, the generation of thought, and, in short, the mental condition observed while awake, complete repose of the brain is characterized by the opposite conditions. It is true that the brain may be rested without sleep, by abstaining from mental effort, by the gratification of certain of the senses, and by mental distraction of various kinds, and that the mind may work to some extent during sleep; but during the period of complete repose—that condition which is so necessary to perfect health and full mental vigor—consciousness and volition are lost, there is no thought, and the brain, which does not receive blood enough to stimulate it to action, is simply occupied in the insensible repair of its substance and is preparing itself for renewed work. The exhaustion of the muscles produces a sense of fatigue of the muscular system, indisposition to muscular exertion, and a desire for rest, not necessarily involving drowsiness. Fatigue of the brain is manifested by indisposition to mental exertion, dullness of the special senses and a desire for sleep. Simple repose will relieve physiological fatigue of muscles; and when a particular set of muscles has been used, the fatigue often disappears when these muscles alone are at rest, though others be brought into action. Sleep, and sleep alone, relieves fatigue of the brain.

During sleep nearly all of the physiological processes, except those directly under the control of the sympathetic nervous system, are diminished in activity. The circulation is slower, and the pulsations of the heart are less frequent, as well as the respiratory movements. These points have already been considered in connection with the physiology of circulation and respiration. Physiologists have but little positive information with regard to the relative activity of the processes of digestion, absorption and secretion, during sleep. The drowsiness which many persons experience after a full meal is probably due to a determination of blood to the alimentary canal and a consequent diminution in the supply to the brain.

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# CHAPTER XXI.

## *SPECIAL SENSES—TOUCH, OLFACTION AND GUSTATION.*

General characters of the special senses—Muscular sense (so called)—Sense of touch—Variations in tactile sensibility in different parts (sense of locality of impressions)—Table of variations measured by the æsthesiometer—Appreciation of temperature—Tactile centre—Olfaction—Nasal fossæ—Schneiderian and olfactory membranes—Olfactory (first nerve)—Physiological anatomy—Olfactory bulbs—Olfactory cells and terminations of the olfactory nerve-fibres—Properties and uses of the olfactory nerves—Mechanism of olfaction—Relations of olfaction to the sense of taste—Reflex acts through the olfactory nerves—Olfactory centre—Gustation—Savors—Nerves of taste—Chorda tympani—Glosso-pharyngeal (ninth nerve)—Physiological anatomy—General properties of the glosso-pharyngeal—Relations of the glosso-pharyngeal nerves to gustation—Mechanism of gustation—Physiological anatomy of the organ of taste—Papillæ of the tongue—Taste-beakers—Connections of the nerves with the organs of taste—Taste centre.

THE description of the nerves thus far has included motion and what is known as general sensibility; and knowledge of these properties of the nervous system has been derived mainly from experiments upon the inferior animals. As regards sensation, the experiments have referred to impressions recognized as painful; and these are conveyed to the centres by nerve-filaments, anatomically as well as physiologically distinct from those which convey to the contractile parts the impulses that give rise to motion. In regard to the sensory nerves, simple impressions only have been described; but it is evident that the filaments of peripheral distribution of these nerves are capable of receiving a variety of impressions, by which, to a certain extent, the form, size, character of surface, density and temperature of objects are recognized. There is also a general appreciation of heat and cold; a sense of resistance, which gives an idea of weight; and finally, there are nerves of peculiar properties, terminating in organs adapted to receive the impressions of smell, taste, sight and hearing.

The senses of olfaction, gustation, vision and audition belong to peculiar organs, provided with nerves which have special properties and usually are not endowed with general sensibility. These nerves have been omitted in the general description of the nervous system, as well as the accessory organs to which they are distributed.

The senses of touch, temperature and pain are all conveyed to the nerve-centres by what have been described as sensory nerves, the touch being perfected in certain parts by peculiar arrangements of the terminal nerve-fibres. Although it is possible that each one of these impressions is transmitted by special and distinct fibres, this is not yet a matter of positive demonstration. The so-called muscular sense, by which weight, resistance etc., are appreciated, undoubtedly depends to a great extent upon the muscular nerves. What are generally recognized as sensory impressions have been thus subdivided. These subdivisions are sufficiently distinct, as far as the character of the sensations themselves are concerned, but as regards their paths of conduction, as before intimated, exact and positive *data* are wanting. It is impossible to study with advantage the different varieties of ordinary sensation in the lower animals, for evident reasons; and physiologists rely mainly upon observations on the human subject, in the form of experiments and of pathological phenomena.

There are two ways of regarding the different varieties of general sensation: One is to look at each as a peculiar impression conveyed by special nerve-fibres, and the other is to regard the nerves of general sensibility as capable of conducting impressions of different kinds. It has never been assumed that special fibres for each variety of sensation have been demonstrated, and it is possible only to reason as to this from what is actually known of the general properties of sensory nerves.

The general sensory nerves are sufficiently distinct in their properties from the true nerves of special sense. The latter convey peculiar impressions only, such as those of sight, hearing, smell and taste. The former, when strongly stimulated or irritated, always convey impressions of pain. Separating, then, all other senses, except the venereal sense, from the true special senses, it is proper to inquire whether it be reasonable or necessary to assume that any of the varieties of general sensation require special nerves for their conduction.

It is well known that a relatively powerful stimulation of a sensory nerve or of sensitive parts is necessary to the production of a painful impression; and it is also well known that very painful impressions overpower impressions of touch, weight, pressure, temperature and the so-called muscular sense. In cases of disease, it is sometimes observed that tactile sensibility is retained in parts that are insensible as regards pain. It is possible that sensory nerve-fibres may become so altered in their properties as to be incapable of conducting painful impressions, while they still conduct sensations that are appreciated only as impressions of contact. This is observed in certain cases of artificial anæsthesia. In hyperæsthesia, or exaggerated sensibility to painful impressions, the tactile sense is necessarily overpowered in a greater or less degree. Impressions made on a sensory nerve in its course are always appreciated as painful, and the pain is referred to the terminal distribution of the nerve, this being a law of sensory perception. There is no sense of contact at the ends of the nerve, and there is no contact. The impression, in order to be perceived at all, must be painful. These facts may be in a measure applied to local impressions produced by extremes of heat and cold or by chemical or electric stimulation of sensitive parts.

The internal organs have as a rule no tactile sensibility, although they may be sensitive; and feeble impressions may not be appreciated, while stronger impressions are painful.

Titillation is the result of unusual, feeble impressions or of slight impressions frequently repeated in the peripheral ends of certain sensory nerves. These impressions are not precisely tactile nor are they painful. They produce peculiar sensations, and they frequently give rise to violent reflex movements, by what is known as a summation of sensory stimulations.

*Muscular Sense (so called).*—It is difficult to define exactly what is meant by the term muscular sense, as it is used by some physiologists. In all probability, the sense which enables one to appreciate the resistance, immobility and elasticity of substances that are grasped or stood upon or which are in any way opposed to the exertion of muscular power, may be greatly modified by education and habit. It is undoubtedly true, however, that general sensibility regulates the action of muscles to a considerable extent. If, for example, the lower extremities be paralyzed as regards sensation, the muscular power remaining intact, frequently the person so affected can not walk unless he be able to see the ground. This difficulty occurs for the reason that the limbs have lost the sense of contact. Many curious examples of this kind are to be found in works upon diseases of the nervous system. One of the most striking is a case communicated to Charles Bell by Dr. Ley. The patient was affected with partial loss of sensibility upon one side of the body, "without, however, any corresponding diminution of power in the muscles of volition, so that she could hold her child in the arm of that side so long as her attention was directed to it; but if surrounding objects withdrew her from the notice of the state of her arm, the flexors gradually relaxed, and the child was in hazard of falling." This is like certain of the phenomena observed in cases of locomotor ataxia. In this disorder there is disease of the posterior white columns of the spinal cord, involving, sometimes, the posterior roots of the spinal nerves, with more or less impairment of general sensibility, the muscular power in some instances being intact. Patients affected in this way frequently are unable to walk or stand without the aid of the sight. One of the most characteristic phenomena is inability to stand when blindfolded; although, with the aid of the sight, the muscles can be made by the will to act with considerable power. Habit and education enable some persons to appreciate with great nicety slight differences in weight; but this is due chiefly to the sense of resistance to muscular effort and has little dependence upon the sense of touch.

In general those parts which are most sensitive to the impressions of touch, as the fingers, enable one to appreciate differences in pressure and weight with greatest accuracy. The sense of simple pressure, unaided by the estimation of weight by muscular effort, generally is more acute upon the left side. Differences in weight can be accurately distinguished when they amount to only one-sixteenth, by employing muscular effort in lifting as well as the sense of pressure; but the sense of pressure alone enables most persons to appreciate a difference of not less than one-eighth. When weights are tested by lifting with the hand, the appreciation of slight differences is more delicate if the weights be successively tested with the same hand than when two weights are placed, one on either hand. When the interval between the two trials is more than forty seconds, slight differences in weight —the difference between fourteen and a half and fifteen ounces (411 and 425 grammes), for example—can not be accurately appreciated. In such trials, it is necessary to have the metals used of the same temperature, for cold metals seem heavier than warm.

## Sense of Touch.

The different modes of termination of the sensory nerves have already been described; and in many instances it is possible to explain, by the anatomical characters of the nerves, the great differences that have been observed in the delicacy of the tactile sensibility in different parts—differences which are very important pathologically as well as physiologically, and which have been studied by Weber, Valentin and others, with great minuteness.

*Variations in the Tactile Sensibility in Different Parts* (*Sense of Locality of Impressions*).—In certain parts of the cutaneous surface the general sensibility is much more acute than in others. For example, a sharp blow upon the face is more painful than a similar injury to other parts; and the eye, as is well known, is peculiarly sensitive. The appreciation of temperature varies in different parts, this probably depending to a great extent upon habitual exposure. Some parts, as the soles of the feet or the axilla, are peculiarly sensitive to titillation. The sense of touch, also, by which the size, form, character of the surface, consistence etc., of objects are appreciated, is developed to a greater degree in some parts than in others. The tips of the fingers generally are used to ascertain those properties of objects revealed by the sense of touch. This sense is capable of education and is almost always extraordinarily developed in persons who are deprived of some other special sense, as sight or hearing. The blind learn to recognize individuals by feeling of the face. A remarkable instance of this is quoted in works on physiology, of the blind sculptor, Giovanni Gonelli, who was said to model excellent likenesses, being guided entirely by the sense of touch. Other instances of this kind are on record. The blind have been known to become proficients in conchology and botany, guided entirely by the touch. It is related of a blind botanist, that he was able to distinguish ordinary plants by the fingers and by the tip of the tongue. It is well known that the blind learn to read with facility by passing the fingers over raised letters but little larger than the letters in an ordinary folio Bible.

An easy method of determining the relative delicacy of the tactile sensibility of different portions of the cutaneous surface was devised a number of years ago (1829) by E. H. Weber. This method consists in the application to the skin, of two fine points, separated from each other by a known distance. The individual experimented upon should be blindfolded, and the points applied to the skin simultaneously. By carefully adjusting the distance between the points, a limit will be reached where the two impressions upon the surface are appreciated as one; *i. e.*, by gradually approximating them, the subject will suddenly feel both points as one, when an instant before, with the points a little farther removed from each other, he distinctly felt two impressions. This gives a measure of the delicacy of the tactile sensibility of different parts. Of course the instrument used may be very simple—a pair of ordinary dividers will answer—but it is convenient to have some ready means of ascertaining the distances between the points. An instrument, consisting simply of a pair of dividers with a graduated bar giving a measure of the separation of the points, is the best, as it combines simplicity, convenience of use and portability. This instrument is called an æthesiometer. The experiments of Weber were made upon his own person. They showed some slight variations with the direction of the line of the two points, but these are not very important. The table which follows is made of selections from the observations of Weber, taking those that are most likely to be useful as a guide in pathological investigations. The experiments of Valentin and others on different persons do not vary much in their results from the figures given in the table.

TABLE OF VARIATIONS IN THE TACTILE SENSIBILITY OF DIFFERENT PORTIONS OF THE SKIN (WEBER).

The tactile sensibility is measured by the greatest distance between two points at which they convey a single impression when applied simultaneously. The measurements are given in lines ($\frac{1}{12}$ of an inch, or a little more than 2 mm.).

| PART OF SURFACE. | Lines. | Mm. |
|---|---|---|
| Tip of tongue | 0·50 | 1·05 |
| Palmar surface of third phalanx of forefinger | 1·00 | 2·10 |
| Red surface of under lip | 2·00 | 4·20 |
| Palmar surface of second phalanges of fingers | 2·00 | 4·20 |
| Dorsal surface of third phalanges of fingers | 3·00 | 6·30 |
| Tip of nose | 3·00 | 6·30 |
| Palmar surface of metacarpus | 3·00 | 6·30 |
| End of great toe | 5·00 | 10·50 |
| Palm of hand | 5·00 | 10·50 |
| Skin of cheek, over buccinator | 5·00 | 10·50 |
| Skin of cheek, over anterior part of malar bone | 7·00 | 14·70 |
| Dorsal surface of first phalanges of fingers | 7·00 | 14·70 |
| Lower part of forehead | 10·00 | 21·00 |
| Back of hand | 14·00 | 29·40 |
| Patella and surrounding part of thigh | 16·00 | 33·60 |
| Dorsum of foot near toes | 18·00 | 37·80 |
| Upper and lower extremities of forearm | 18·00 | 37·80 |
| Upper and lower extremities of leg | 18·00 | 37·80 |
| Penis | 18·00 | 37·80 |
| Acromion and upper part of arm | 18·00 | 37·80 |
| Gluteal region and neighboring part of thigh | 18·00 | 37·80 |
| Middle of forearm where its circumference is greatest | 30·00 | 63·00 |
| Middle of thigh where its circumference is greatest | 30·00 | 63·00 |

By comparing the distribution of the tactile corpuscles with the results given in the table, it will be seen that the sense of touch is most acute in those situations in which the corpuscles are most abundant. In the space of a little more than $\frac{1}{12}$ of an inch (2·2 mm.) square, on the palmar surface of the third phalanx of the index-finger, Meissner counted the greatest number of corpuscles; viz., one hundred and eight. In this situation the tactile sensibility is more acute than in any other part of the skin, the mean distance indicated by the æsthesiometer being 0·603 of a line, or 1·27 mm. (Valentin). In the same space on the second phalanx, forty corpuscles were counted, the æsthesiometer marking 1·558 line, or 3·27 mm. (Valentin), this part ranking next in tactile sensibility after the red surface of the lips. One can readily understand how the tactile corpuscles, embedded in the amorphous substance of the cutaneous papillæ, might increase the delicacy of appreciation of slight impressions, by presenting hard surfaces against which the nerve-filaments can be pressed.

As regards those portions of the general cutaneous surface in which no tactile corpuscles have been demonstrated, it is not easy to connect the variations in the tactile sensibility with the nervous distribution, as little is known of the comparative richness of the terminal nervous filaments in these situations.

*Appreciation of Temperature.*—It is not known that the sense of temperature, either of the surrounding medium or of bodies applied to different parts of the skin, is appreciated through any nerves other than those of general sensibility or that there is any special arrangement of the terminations of certain of the nerves connected with this sense. As regards the general temperature, the sense is relative and is much modified by habit. This statement needs no explanation. As is well known, what is cold for an inhabitant of the torrid zone would be warm for one accustomed to an excessively cold climate. Habitual exposure also modifies the sense of temperature. Many persons not in the habit of dressing warmly suffer but little in extremely cold weather. Those who habitually expose the hands or even the feet to cold, render these parts comparatively insensible to temperature; and the same is true of those who often expose the hands, face or other parts to heat. The variations in the sensibility of different parts of the surface to temperature depend, also, upon special properties of the parts themselves. The differences, however, are not so marked as to be of any great importance, and the experiments made upon this point are simply curious.

The experiments of Weber and others show that the skin is the chief organ for the appreciation of temperature, if the mouth, palate, vagina and rectum, by which the differences between warm and cold substances is readily distinguished, be excepted. In several instances in which larger portions of the skin were destroyed by burns and other injuries, experiments have been made by applying spatulas of different temperatures. In one of these, a spatula plunged in water at 48° to 55° Fahr. (9° to 12° C.) was applied to a denuded surface, and again, a spatula at 113° to 122° Fahr. (45° to 50° C.). When the patient was requested to tell which was the warmer, the answers were as frequently incorrect as they were correct; but the discrimination was easy and certain when the applications were made to the surrounding healthy skin. When applications at a higher temperature were made to the denuded part, the patient suffered only pain.

The venereal sense is unlike any other sensation, and is general as well as referable to the organs of generation. In this connection, however, it is important to note that the tactile sensibility of the palmar surface of the third phalanx of the fingers, measured by the æsthesiometer, compared with the sensibility of the penis, is as 0·802 to 0·034, or between twenty-three and twenty-four times greater.

Ferrier has described a diffused tactile centre in the "hippocampal region," the action of which is crossed; but the observations to determine the loss of the sense of touch after destruction of this part, which were made on monkeys, are by no means satisfactory. It must be very difficult to study tactile sensibility in the inferior animals.

## Olfaction.

The nerves directly connected with the senses of olfaction, vision and audition, have little or no general sensibility. As regards the olfactory nerves, the parts to which they are distributed are so largely supplied with branches from the fifth, that it is difficult to determine the fact of their sensibility or insensibility to ordinary impressions. The olfactory nerves, however, are distributed to the mucous membrane of that portion only of the nasal cavity, endowed with the special sense of smell.

*Nasal Fossæ.*—The two irregularly shaped cavities in the middle of the face, opening in front by the anterior nares and connected with the pharynx by the posterior nares, are called the nasal fossæ. The membrane lining these cavities is generally called the Schneiderian mucous membrane, and sometimes, the pituitary membrane. This membrane is closely adherent to the fibrous coverings of the bones and cartilages by which the nasal fossæ are bounded, and it is thickest over the turbinated bones. It is continuous with the membrane lining the pharynx, the nasal duct and lachrymal canals, the Eustachian tube, the frontal, ethmoidal and sphenoidal sinuses and the antrum. There are openings leading from the nasal fossæ to all of these cavities.

The essential organ of olfaction is the mucous membrane lining the upper half of the nasal fossæ. Not only has it been shown anatomically that this part alone receives the terminal filaments of the olfactory nerves, but physiological experiments have demonstrated that it is the only part capable of appreciating odorous impressions. If a tube be introduced into the nostril, placed horizontally over an odorous substance so that the emanations can not penetrate its caliber, no odor is perceived, though the membrane below the end of the tube might receive the emanations; but if the tube be directed toward the odorous substance, so that the emanations can penetrate to the upper portion of the nares, the odor is immediately appreciated.

That portion of the lining of the nasal fossæ, properly called the olfactory membrane, extends from the cribiform plate of the ethmoid bone downward a little less than an inch (25 mm.). It is soft and friable, very vascular, thicker than the rest of the Schneiderian membrane, and in man, it has rather a yellowish color. It is covered by long, delicate, columnar cells, nucleated, and each one provided with three to eight ciliary processes, the movements of which are from before backward. The olfactory membrane is provided with a large number of long, racemose, mucous glands, which secrete a fluid that keeps the surface moist, a condition essential to the accurate perception of odorous impressions.

### Olfactory (First Nerve).

The apparent origin of the olfactory nerve is by three roots, from the inferior and internal portion of the frontal lobe of the cerebrum, in front of the anterior perforated space. The three roots are an external and an internal white root, and a middle root composed of gray matter. The external white root is long and delicate, passing outward, across the fissure of Sylvius, to the temporo-sphenoidal lobe. The internal white root is thicker and shorter than the external root, and it arises from the most posterior portion of the frontal lobe. The middle, or gray root arises from a little eminence of gray matter situated on the posterior and inner portion of the inferior surface of the frontal lobe.

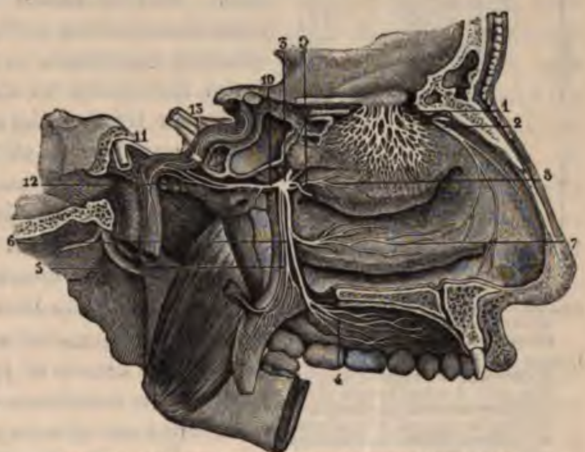

Fig. 235.—*Olfactory ganglion and nerves* (Hirschfeld).

1, *olfactory ganglion and nerves*; 2, branch of the nasal nerve; 3, spheno-palatine ganglion; 4, 7, branches of the great palatine nerve; 5, posterior palatine nerve; 6, middle palatine nerve; 8, 9, branches from the spheno-palatine ganglion; 10, 11, 12, Vidian nerve and its branches; 13, external carotid branch, from the superior cervical ganglion.

The deep origin of these three roots of the olfactory nerves is still a matter of discussion. The external root passes through the gray substance of the island of Reil, to a gray nucleus in the temporo-sphenoidal lobe, in front of the pes hippocampi. The fibres of the middle root have not been traced farther than the gray eminence from which it arises. The fibres of the internal root probably are connected with the fibres of the gyrus fornicatus. The three roots converge to form a single cord at the inner boundary of the fissure of Sylvius. This cord passes forward and slightly inward, in a deep groove between two convolutions on the under surface of the frontal lobe, covered by the arachnoid membrane, to the ethmoid bone. This portion of the nerve is soft and friable. It is composed of both white and gray matter, the proportions being about two-thirds of the former to one-third of the latter. The gray substance, derived from the gray root, is situated at the upper portion of the nerve, the white substance occupying the inferior and the lateral portions.

By the side of the crista galli of the ethmoid bone, the nerve-trunk expands into an oblong ganglion called the olfactory bulb. This is grayish in color, excessively soft, and contains the ordinary ganglionic elements. From the olfactory bulb, fifteen to eighteen nervous filaments are given off, which pass through the foramina in the cribriform plate of the ethmoid bone. These filaments are composed entirely of nerve-fibres, and are quite resisting, owing to fibrous elements prolonged from the dura mater. It is strictly proper, perhaps, to regard these as the true olfactory nerves, the cord leading from the olfactory bulb to the cerebrum being properly a commissure. Having passed through the cribriform plate, the olfactory nerves are distributed to the olfactory membrane, in three groups: an inner group, distributed to the mucous membrane of the upper third of the septum; a middle group, to the upper portion of the nasal fossæ; and an outer group, to the mucous membrane covering the superior and middle turbinated bones and a portion of the ethmoid.

FIG. 236.—*Terminal filaments of the olfactory nerves; magnified 30 diameters* (Kölliker).

1, from the frog.—*a*, epithelial cell of the olfactory region; *b*, olfactory cell; 2, small branch of the olfactory nerve of the frog, separating at one end into a brush of varicose fibrils. 3, olfactory cell of the sheep.

The mode of termination of the olfactory nerves differs from that of the ordinary sensory nerves, and is peculiar and characteristic, as it is in the other organs of special sense. The olfactory mucous membrane contains terminal nerve-cells, called the olfactory cells, which are situated between the cells of epithelium. These are long, delicate, spindle-shaped, varicose structures, each one containing a clear, round nucleus. In the frog there is a fine, hair-like process projecting from each cell, beyond the mucous membrane, which has not been observed in man or the mammalia. The delicacy of the structures entering into the composition of the olfactory membrane renders the investigation of the termination of its nervous filaments exceedingly difficult.

*Properties and Uses of the Olfactory Nerves.*—It is almost certain that the olfactory nerves possess none of the general properties of the ordinary nerves belonging to the cerebro-spinal system, and are endowed with the special sense of smell alone. The filaments coming from the olfactory bulbs and distributed to the pituitary membrane have not been exposed and stimulated in living animals; but experiments upon the nerves behind the olfactory bulbs show that they are insensible to ordinary impressions. Attempts have been made to demonstrate, in the human subject, the special properties of these nerves, by passing an electric current through the nostrils; but the situation of the nerves is such that these observations are of necessity indefinite and unsatisfactory.

Among the experiments upon the higher orders of animals, in which the olfactory nerves have been divided, may be cited, as open to no objections, those of Vulpian and Philipaux, upon dogs. It is well known that the sense of smell usually is very acute in these animals. Upon dividing or extirpating the olfactory bulbs, "after the animal had completely recovered, it was deprived of food for thirty-six or forty-eight hours; then, in its absence, a piece of cooked meat was concealed in a corner of the laboratory. Animals, successfully operated upon, then taken into the laboratory, never found the bait; and nevertheless, care had been taken to select hunting-dogs." This experiment is conclusive; more so than those in which animals deprived of the olfactory bulbs were shown to eat fæces without disgust, for this sometimes occurs in dogs that have not been multilated.

Comparative anatomy shows that the olfactory bulbs generally are developed in proportion to the acuteness of the sense of smell. Pathological facts show, in the human subject, that impairment or loss of the olfactory sense is coincident with injury or destruction of these ganglia. Cases have been reported in which the sense of smell was lost or impaired from injury to the olfactory nerves. In nearly all of the cases on record, the general sensibility of the nostrils was not affected.

*Mechanism of Olfaction.*—Substances that have odorous properties give off material emanations, which must come in contact with the olfactory membrane before their peculiar odor is appreciated. This membrane is situated high up in the nostrils, is peculiarly soft, is abundantly provided with glands, by the secretions of which its surface is kept in proper condition, and it presents the peculiar nerve-terminations of the olfactory filaments.

In experimenting upon the sense of smell it has been found difficult to draw an exact line of distinction between impressions of general sensibility and those which attack the special sense, or in other words, between irritating and odorous emanations; and the vapors of ammonia, acetic acid, nitric acid etc., undoubtedly possess irritating properties which overpower their odorous qualities. It is unnecessary in this connection to discuss the different varieties of odors recognized by some of the earlier writers, as the fragrant, aromatic, fetid, nauseous etc., distinctions sufficiently evident from their mere enumeration; and it is plain enough that there are emanations, like those from delicately scented flowers, which are easily recognizable by the sense of smell, while they make no impression upon the ordinary sensory nerves. The very marked individual differences in the delicacy of the olfactory organs in the human subject and in different animals are evidence of this fact. Hunting-dogs recognize odors to which most persons are absolutely insensible; and certain races of men are said to possess a remarkable delicacy of the sense of smell. Like the other special senses, olfaction may be cultivated by attention and practice, as is exemplified in the delicate discrimination of wines, qualities of drugs etc., by experts.

After what has been said concerning the situation of the true olfactory membrane in the upper part of the nasal fossæ and the necessity of particles impinging upon this membrane in order that their odorous properties may be appreciated, it is almost unnecessary to state that the passage of odorous emanations to this membrane by inspiring through the nostrils is essential to olfaction, so that animals or men, after division of the trachea, being unable to pass the air through the nostrils, are deprived of the sense of smell. The act of inhalation through the nose is an illustration of the mechanism by which the odorous particles may be brought at will in contact with the olfactory membrane.

It is a curious point to determine whether the sense of smell be affected by odors passing from within outward through the nasal fossæ. Persons who have offensive emanations from the respiratory organs usually are not aware, from their own sensations, of any disagreeable odor. This fact is explained by Longet on the supposition that the olfactory membrane becomes gradually accustomed to the odorous impression, and therefore it is not appreciated. This is an apparently satisfactory explanation, for it could hardly be supposed that the direction of the emanations, provided they came in contact with the membrane, could modify their effects. Longet has cited a case of cancer of the stomach, in which the vomited matters were exceedingly fetid. At first, the patient, when he expired the gases from the stomach through the nostrils, perceived a disagreeable odor at each expiration; but little by little this impression disappeared.

*Relations of Olfaction to the Sense of Taste.*—The relations of the sense of smell to gustation are very intimate. In the appreciation of delicate shades of flavor, it is well known that the sense of olfaction plays so important a part, that it can hardly be separated from gustation. The common practice of holding the nose when disagreeable remedies are swallowed is an illustration of the connection between the two senses. In most cases of anosmia there is inability to distinguish delicate flavors; and patients can distinguish by the taste, only sweet, saline, acid and bitter impressions.

It is undoubtedly true that the delicacy of the sense of taste is lost when the sense of smell is abolished. The experiment of tasting wines blindfolded and with the nostrils plugged, and the partial loss of taste during a severe coryza, are sufficiently familiar illustrations of this fact. In the great majority of cases, when there is complete anosmia, the taste is sensibly impaired; and in cases in which this does not occur, it is probable that the savory emanations pass from the mouth to the posterior portion of the nasal fossæ, and that here the mucous membrane is not entirely insensible to special impressions.

It is unnecessary, in this connection, to describe fully the reflex phenomena which follow impressions made upon the olfactory membrane. The odor of certain sapid substances, under favorable conditions, will produce an abundant secretion of saliva and even of gastric juice, as has been shown by experiments upon animals. Other examples of the effects of odorous impressions of various kinds are sufficiently familiar.

According to Ferrier, the olfactory centre is on the inner surface of the anterior extremity of the unicate gyrus; but this location of the centre is not regarded as definitely determined. Stimulation of this part in monkeys simply produces peculiar movements of the nostril and lip of the same side.

## GUSTATION.

The special sense of taste gives the appreciation of what is known as the savor of certain substances introduced into the mouth; and this sense exists, in general terms, in parts supplied by filaments from the lingual branch of the fifth and the glosso-pharyngeal nerves.

It is assumed by some physiologists, that the true tastes are quite simple, presenting the qualities which are recognized as sweet, acid, saline and bitter; while the more delicate shades of what are called flavors nearly always involve olfactory impressions, which it is difficult to separate entirely from gustation. Applying the term savor exclusively to the quality which makes an impression upon the sense of taste, it is evident that the sensation is special in its character and different from the tactile sensibility of the parts involved and from the sensation of temperature. The terminal filaments of the gustatory nerves are impressed by the actual contact of savory substances, which must of necessity be soluble. To a certain extent there is a natural classification of savors, some of which are agreeable, and others, disagreeable; but even this distinction is modified by habit, education and various other circumstances. Articles that are unpleasant in early life often become agreeable in later years. Inasmuch as the taste is to some extent an expression of the nutritive demands of the system, it is found to vary under different conditions. Chlorotic females, for example, frequently crave the most unnatural articles, and their morbid tastes may disappear under appropriate treatment. Inhabitants of the frigid zones crave fatty articles of food and will even drink rancid oils with avidity. Patients often become accustomed to the most disagreeable remedies and take them without repugnance. Again, the most savory dishes may even excite disgust, when the sense of taste has become cloyed, while abstinence sometimes lends a delicious flavor to the simplest articles of food. The taste for certain articles certainly is acquired, and this is almost always true of tobacco, now so largely used in civilized countries.

Any thing more than the simplest classification of savors is difficult if not impossible. It is easy to recognize that certain articles are bitter or sweet, empyreumatic or insipid, acid or alkaline, etc., but beyond these simple distinctions, the shades of difference are closely connected with olfaction and are too delicate and too many for detailed description. Some persons are comparatively insensible to nice distinctions of taste, while others recognize with facility the most delicate differences. Strong impressions may remove for a time the appreciation of less powerful and decided flavors. The tempting of the appetite by a proper gradation of gustatory and odorous impressions is illustrated in the modern *cuisine*, which aims at an artistic combination and succession of dishes and wines, so that the agreeable sensations are prolonged to the utmost limit. This may often be regarded as a violation of strictly hygienic principles, but it none the less exemplifies the cultivation of the sense of taste.

*Nerves of Taste.*—Two nerves, the chorda tympani and the gloss-pharyngeal, are endowed with the sense of taste. These nerves are distributed to distinct portions of the gustatory organ. The chorda tympani has already been referred to as one of the branches of the facial; the glosso-pharyngeal has not yet been described.

*Chorda Tympani.*—In the description already given of the facial, the chorda tympani is spoken of as the fourth branch. It passes through the tympanum, between the ossicles of the ear, and joins the inferior maxillary division of the fifth, at an acute angle, between the two pterygoid muscles, becoming so closely united with it that it can not be followed farther by dissection. The filaments of this branch probably originate from the intermediary nerve of Wrisberg.

The course of the filaments of the chorda tympani, after this nerve has joined the fifth, is shown by the effect upon the sense of taste and the alteration of the nerve-fibres following its division. Vulpian and Prevost, by the so-called Wallerian method, after dividing the chorda tympani, found degenerated fibres at the terminations of the lingual branch of the fifth, in the mucous membrane of the tongue, the fibres being examined ten days or more after the section. Observations upon the sense of taste show that the chorda tympani is distributed to the anterior two-thirds of the tongue.

The general properties of the chorda tympani have been ascertained only by observations made after its paralysis or division. All experiments in which a stimulus has been applied directly to the nerve in living animals have been negative in their results. According to Longet, when the nerve has been isolated as completely as possible and all reflex action is excluded, its stimulation produces no movement in the tongue.

In cases of facial palsy in which the lesion affects the root so deeply as to involve the chorda tympani, there is loss of taste in the anterior two-thirds of the tongue, tactile sensibility being unaffected; and many cases illustrating this fact have been recorded. Aside from cases of paralysis of the facial with impairment of taste, in which the general sensibility of the tongue is intact, instances are on record of affections of the fifth pair, in which the tongue was absolutely insensible to ordinary impressions, the sense of taste being preserved. A number of such cases have been reported, which show conclusively that the fifth pair presides over general sensibility only, and that it is not a gustatory nerve, except by virtue of filaments derived from the chorda tympani.

Passing from the consideration of pathological facts to experiments upon living animals, the results are equally satisfactory. Although it is somewhat difficult to observe impairment of taste in animals, Bernard and others have succeeded in training dogs and cats so as to observe the effects of colocynth and various sapid substances applied to the tongue. In a great number of experiments of this kind, it has been observed that after section of the chorda tympani, or of the facial so as to involve the chorda tympani, the sense of taste is abolished in the anterior two-thirds of the tongue on the side of the section. In a case reported by Moos, the introduction of an artificial membrana tympani in the human subject was followed by loss of taste upon the corresponding side of the tongue, and upon both sides, when a membrane was introduced into each ear. This disappeared when the membranes were removed, and the phenomena were referred to pressure upon the chorda tympani. Other instances of this kind are on record.

As regards the gustatory properties of the anterior two-thirds of the tongue, certainly in the human subject, it may be stated without reserve, that these properties depend upon the chorda tympani, its gustatory filaments being derived from the facial and taking their course to the tongue with the lingual branch of the inferior maxillary division of the fifth. In addition, the lingual branch of the fifth contains filaments, derived from the large root of this nerve, which give general sensibility to the mucous membrane.

## Glosso-Pharyngeal (Ninth Nerve).

The glosso-pharyngeal is distributed to those portions of the gustatory mucous membrane not supplied by filaments from the chorda tympani. It is undoubtedly a nerve of taste; and the question of its other uses will be considered in connection with its general properties, as well as the differences between this nerve and the chorda tympani.

*Physiological Anatomy.*—The apparent origin of the glosso-pharyngeal is from the groove between the olivary and restiform bodies of the medulla oblongata, between the roots of the auditory nerve above and the pneumogastric below. The deep origin is in a gray nucleus in the lower part of the floor of the fourth ventricle, between the nucleus of the auditory nerve and the nucleus of the pneumogastric. From this origin the filaments pass forward and outward, to the posterior foramen lacerum, by which the nerve emerges with the pneumogastric, the spinal accessory and the internal jugular vein. At the upper portion of the foramen, is a small ganglion, the jugular ganglion, including only a portion of the root. Within the foramen, is the main ganglion, including all of the filaments of the trunk, called the petrous ganglion, or the ganglion of Andersch.

At or near the ganglion of Andersch the glosso-pharyngeal usually receives a delicate filament from the pneumogastric. This communication is sometimes wanting. The same may be said of a small filament passing to the glosso-pharyngeal from the facial, which is not constant. Branches from the glosso-pharyngeal go to the otic ganglion and to the carotid plexus of the sympathetic.

The distribution of the glosso-pharyngeal is quite extensive. The tympanic branch, the nerve of Jacobson, arises from the anterior and external part of the ganglion of Andersch, and enters the cavity of the tympanum, where it divides into six branches. Of these six branches, two posterior are distributed to the mucous membrane of the fenestra rotunda and the membrane surrounding the fenestra ovalis; two anterior are distributed, one to the carotid canal, where it anastomoses with a branch from the superior cervical ganglion, and the other to the mucous membrane of the Eustachian

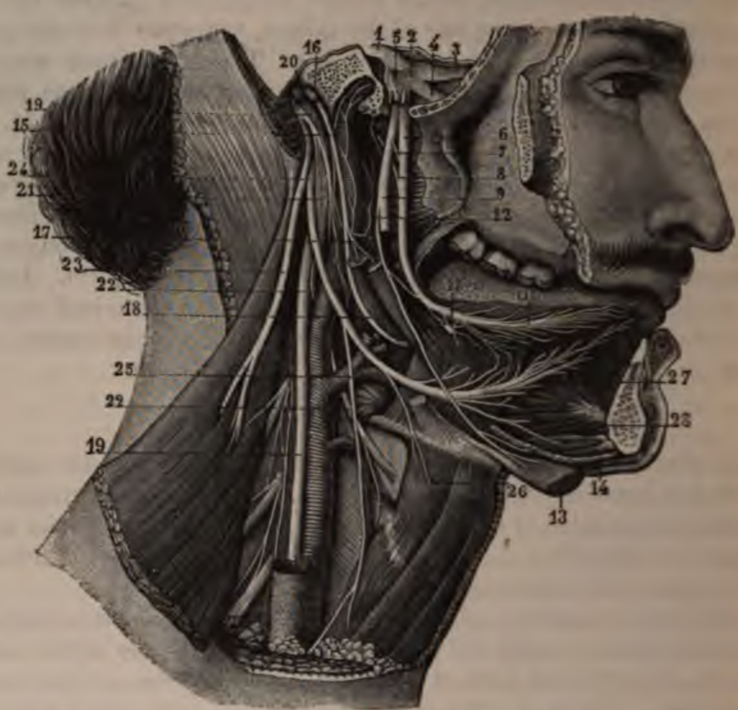


FIG. 237.—*Glosso-pharyngeal nerve* (Sappey).

1, large root of the fifth nerve; 2, ganglion of Gasser; 3, ophthalmic division of the fifth; 4, superior maxillary division; 5, inferior maxillary division; 6, 10, *lingual branch of the fifth, containing the filaments of the chorda tympani*; 7, branch from the sublingual to the lingual branch of the fifth; 8, *chorda tympani*; 9, inferior dental nerve; 11, submaxillary ganglion; 12, mylo-hyoid branch of the inferior dental nerve; 13, anterior belly of the digastric muscle; 14, section of the mylo-hyoid muscle; 15, 18, *glosso-pharyngeal nerve*; 16, *ganglion of Andersch*; 17, *branches from the glosso-pharyngeal to the stylo-glossus and the stylo-pharyngeus muscles*; 19, 19, pneumogastric; 20, 21, ganglia of the pneumogastric; 22, 22, superior laryngeal nerve; 23, spinal accessory; 24, 25, 26, 27, 28, sublingual nerve and branches.

tube; two superior branches are distributed to the otic ganglion and, as is stated by some anatomists, to the spheno-palatine ganglion.

A little below the posterior foramen lacerum the glosso-pharyngeal sends branches to the posterior belly of the digastric and to the stylo-hyoid muscle. There is also a branch which joins a filament from the facial to the stylo-glossus.

Opposite the middle constrictor of the pharynx three or four branches join branches from the pneumogastric and the sympathetic, to form together the pharyngeal plexus. This plexus contains a number of ganglionic points, and filaments of distribution from the three nerves go to the mucous membrane and to the constrictors of the pharynx. The mucous membrane probably is supplied by the glosso-pharyngeal. It is probable, also, that the muscles of the pharynx are supplied by filaments from the pneumogastric, which are derived originally from the spinal accessory.

Near the base of the tongue branches are sent to the mucous membrane covering the tonsils and the soft palate.

The lingual branches penetrate the tongue about midway between its border and centre, are distributed to the mucous membrane at its base and are connected with certain of the papillæ.

*General Properties of the Glosso-Pharyngeal.*—To ascertain the general properties of this nerve, it must be stimulated at its root, before it has contracted anastomoses with other nerves, and the nerve must be divided in order to avoid reflex phenomena. Taking these precautions it has been found that stimulation of the peripheral end of the nerve does not give rise to muscular movements (Longet). There can be no doubt of the fact that the nerve is sensory, although its sensibility is somewhat dull. In experiments in which the nerve has seemed to be insensible to ordinary impressions, it is probable that the animals operated upon had been exhausted more or less by pain and loss of blood in the operation of exposing the nerve, which, it is well known, abolish the sensibility of some of the nerves.

Experiments upon the glosso-pharyngeal are not very definite and satisfactory in their results as regards the general sensibility of the base of the tongue, the palate and the pharynx. The sensibility of these parts seems to depend chiefly upon branches of the fifth, passing to the mucous membrane, through Meckel's ganglion. Experiments show, also, that the reflex phenomena of deglutition take place mainly through these branches of the fifth, and that the glosso-pharyngeal has little or nothing to do with the process. In fact after division of both glosso-pharyngeal nerves, deglutition does not seem to be affected.

*Relations of the Glosso-Pharyngeal Nerves to Gustation.*—Relying upon experiments on the inferior animals, particularly dogs, it seems certain that there are two nerves presiding over the sense of taste: The chorda tympani gives this sense to the anterior two-thirds portion of the tongue exclusively; the glosso-pharyngeal supplies this sense to the posterior portion of the tongue; the chorda tympani seems to have nothing to do with general sensibility; while the glosso-pharyngeal is an ordinary sensory nerve, as well as a nerve of special sense.

Where there are such differences in the delicacy of the sense of taste as exist usually in different individuals, it must be difficult to describe with accuracy delicate shades of savor, particularly in alimentary substances; but the distinct impressions of acidity or of bitter quality are easily recognizable. It is certain, however, that saline, acid and styptic tastes are best appreciated through the chorda tympani, and that sweet, alkaline, bitter and metallic impressions are received mainly by the glosso-pharyngeal.

*Mechanism of Gustation.*—Articles which make the special impression upon the gustatory organ are in solution; introduced into the mouth, they increase the flow of saliva, the reflex action involving chiefly the submaxillary and sublingual glands; there is usually more or less mastication, which increases the flow of the parotid saliva; and during the acts of mastication and the first stages of deglutition, the sapid substances are distributed over the gustatory membrane, so extensively, indeed, that it is difficult to exactly locate the seat of the special impression. In this way, by the movements of the tongue, aided by an increased flow of saliva, the actual contact of the savory articles is rapidly effected. The thorough distribution of these substances over the tongue and the mucous membrane of the general buccal cavity leads to some confusion in the appreciation of the special impressions; and in order to ascertain if different portions of the membrane possess different properties, it is necessary to make careful experiments, limiting the points of contact as exactly as possible. This has been done, with the result of showing that the true gustatory organ is quite restricted in its extent.

*Physiological Anatomy of the Organ of Taste.*—Anatomical and physiological researches have shown that, at least in the human subject, the organ of taste probably is confined to the dorsal surface of the tongue and the lateral portion of the soft palate. The upper surface of the tongue presents a large number of special papillæ, called, in contradistinction to the filiform papillæ, fungiform and circumvallate. These are not found on its under surface or anywhere except on the superior portion; and it is now well established that the circumvallate and fungiform papillæ alone contain the organs of taste. Experiments upon the gustatory organs, by the application of solutions to different parts through fine, glass

FIG. 238.—*Papillæ of the tongue* (Sappey).

1, 1, circumvallate papillæ; 2, median circumvallate papilla, which entirely fills the foramen cæcum; 3, 3, 3, 3, fungiform papillæ; 4, 4, filiform papillæ; 5, 5, vertical folds and furrows of the border of the tongue; 6, 6, 6, 6, glands at the base of the tongue; 7, 7, tonsils; 8, epiglottis; 9, median glosso-epiglottidean fold.

tubes, have shown that the mucous membrane around a papilla has no gustatory sensibility, but that different savors can be distinguished when a single papilla is touched (Camerer).

In Fig. 238, which represents the dorsal surface of the tongue, the large, circumvallate papillæ, usually seven to twelve in number, are seen in the form of an inverted V, occupying the base of the tongue. The fungiform papillæ are scattered over the surface but are most abundant at the point and near the borders. Both of these varieties of papillæ are distinguishable by the naked eye.

The circumvallate papillæ simply are enlarged, fungiform papillæ, each one surrounded by a circular ridge, or wall, and covered by small, secondary

FIG. 239.—*Medium-sized circumvallate papilla* (Sappey).

FIG. 240.—*Fungiform, filiform, and hemispherical papillæ* (Sappey).

FIG. 239.—1, papilla, the base only being apparent (it is seen that the base is covered with secondary papillæ); 2, groove between the papilla and the surrounding wall; 3, 3, wall of the papilla.

FIG. 240.—1, 1, two fungiform papillæ covered with secondary papillæ; 2, 2, 2, filiform papillæ; 3, a filiform papilla, the prolongations of which are turned outward; 4, a filiform papilla with vertical prolongations; 5, 5, small filiform papillæ with the prolongations turned inward; 6, 6, filiform papillæ with striations at their bases; 7, 7, hemispherical papillæ, slightly apparent, situated between the fungiform and the filiform papillæ.

papillæ. The fungiform papillæ have each a short, thick pedicle and an enlarged, rounded extremity. According to Sappey, one hundred and fifty to two hundred of these can easily be counted. These, also, present small, secondary papillæ on their surface. When the mucous membrane of the tongue is examined with a low magnifying power, particularly after maceration in acetic or in dilute hydrochloric acid, their structure is readily observed. They are abundantly supplied with blood-vessels and nerves.

Several glandular structures are found beneath the mucous membrane of the tongue. On either side of the frenum, near the point, is a gland about three-quarters of an inch (20 mm.) long and one-third of an inch (8·5 mm.) broad, which has five or six little openings on the under surface of the tongue (Blandin and Nuhn). Near the taste-beakers, are small, racemose glands, which discharge a watery secretion, by minute ducts which open into the grooves within the walls of the circumvallate papillæ (Ebner).

*Taste-Beakers.*—Lovén and Schwalbe (1867) described, under this name, peculiar structures which are supposed to be the true organs of taste. They are found on the lateral slopes of the circumvallate papillæ and occasionally on the fungiform papillæ. Their structure is very simple. They consist of flask-like collections of spindle-shaped cells, which are received into little excavations in the epithelial covering of the mucous membrane, the bottom resting upon the connective-tissue layer. Their form is ovoid, and at the neck of each flask, is a rounded opening, called the taste-pore. Their length is $\frac{1}{350}$ to $\frac{1}{300}$ of an inch (71 to 83 $\mu$), and their transverse diameter, about $\frac{1}{600}$ of an inch (41 $\mu$). The cavity of the taste-beakers is filled with cells, of which two kinds are described. The first variety, the outer cells, or the cover-cells, are spindle-shaped, and curved to correspond to the wall of the beaker. These come to a point at the taste-pore. In the interior of the beaker are elongated cells, with large, clear nuclei, which are called taste-cells. According to Engelmann, delicate, hair-like processes are connected with the taste-cells and extend through the taste-pores, in the form of very fine filaments.

FIG. 241.—*Taste-beakers, from the lateral taste-organ of the rabbit* (Engelmann).

Bodies similar to the taste-beakers have been found on the papillæ of the soft palate and uvula, the mucous membrane of the epiglottis and some parts of the top of the larynx. As regards these structures in the tongue, it has been found that four or five months after section of the glosso-pharyngeal on one side in rabbits, the taste-buds on the corresponding side of the posterior portion of the tongue disappear, while they remain perfect on the sound side (Vintschgau and Hönigschmied).

According to the views of those who have described the so-called taste-beakers, sapid solutions find their way into the interior of these structures through the taste-pores and come in contact with the taste-cells, these cells being directly connected with the terminal filaments of the gustatory nerves.

Ferrier has described a taste-centre near the so-called olfactory centre in the unicate gyrus; but his observations are not very definite, and the location of a centre for gustation must be regarded as undetermined.

# CHAPTER XXII.

## *VISION.*

General considerations—Optic (second nerve)—General properties of the optic nerves—Physiological anatomy of the eyeball—Sclerotic coat—Cornea—Choroid coat—Ciliary muscle—Iris—Pupillary membrane—Retina—Crystalline lens—Aqueous humor—Chambers of the eye—Vitreous humor—Summary of the anatomy of the globe—The eye as an optical instrument—Certain laws of refraction, dispersion etc., bearing upon the physiology of vision—Refraction by lenses—Visual purple and visual yellow and accommodation of the eye for different degrees of illumination—Formation of images in the eye—Mechanism of refraction in the eye—Astigmatism—Movements of the iris—Direct action of light upon the iris—Action of the nervous system upon the iris—Mechanism of the movements of the iris—Accommodation of the eye for vision at different distances—Changes in the crystalline lens in accommodation—Changes in the iris in accommodation—Erect impressions produced by images inverted upon the retina—Field of indirect vision—The perimeter—Binocular vision—Corresponding points—The horopter—Duration of luminous impressions (after-images)—Irradiation—Movements of the eyeball—Muscles of the eyeball—Centres for vision—Parts for the protection of the eyeball—Conjunctival mucous membrane—Lachrymal apparatus—Composition of the tears.

THE chief important points to be considered in the physiology of vision are the following:

1. The physiological anatomy and the general properties and uses of the optic nerves.
2. The physiological anatomy of the parts essential to correct vision.
3. The laws of refraction, diffusion etc., bearing upon the physiology of vision.
4. The action of the different parts of the eye in the production and appreciation of correct images.
5. Binocular vision.
6. The physiological anatomy and uses of accessory parts, as the muscles which move the eyeball.
7. The physiological anatomy and uses of the parts which protect the eye, as the lachrymal glands, eyelids etc.

### OPTIC (SECOND NERVE).

The bands which pass from the tubercula quadrigemina to the eyes are divided into the optic tracts, which extend from the tubercula on either side to the commissure, or chiasm, the chiasm, or the decussating portion, and the optic nerves, which pass from the chiasm to the eyes.

The optic tracts arise each one by two roots, internal and external. The internal roots, which are the smaller, arise from the anterior tubercula quadrigemina, and pass through the internal corpora geniculata, to the optic chiasm. The external roots, which are the larger, arise from the posterior part of the optic thalami, pass to the external corpora geniculata, from which they receive fibres, and thence to the chiasm.

Partly by anatomical researches (Wernicke) and partly by experiments on the cerebral cortex in the lower animals and pathological observations on the human subject, it has been shown that fibres from the apparent origin of the optic tracts pass backward to the gray matter of the occipital lobes of the cerebrum. It has also been stated by Stilling that fibres pass to the medulla oblongata, extend down as far as the decussation of the pyramids, and probably are concerned in the reflex movements of the iris.

FIG. 242.—*Optic tracts, commissure and nerves* (Hirschfeld).

1, infundibulum; 2, *corpus cinereum*; 3, corpora albicantia; 4, cerebral peduncle; 5, pons Varolii; 6, *optic tracts and nerves, decussating at the commissure, or chiasm*; 7, motor oculi communis; 8, patheticus; 9, fifth nerve; 10, motor oculi externus; 11, facial nerve; 12, auditory nerve; 13, nerve of Wrisberg; 14, glosso-pharyngeal nerve; 15, pneumogastric; 16, spinal accessory; 17, sublingual nerve.

The two roots of each optic tract unite above the external corpus geniculatum, forming a flattened band, which takes an oblique course around the under surface of the crus cerebri, to the optic commissure.

The optic commissure, or chiasm, is situated just in front of the corpus cinereum, resting upon the olivary process of the sphenoid bone. As its name implies, this is the point of union between the nerves of the two sides. At the commissure the fibres from the optic tracts take three directions; and in addition, the commissure contains filaments passing from one eye to the other, which have no connection with the optic tracts. The four sets of fibres in the optic commissure are the following:

1. Decussating fibres, passing from the optic tract upon either side to the eye of the opposite side. The greatest part of the fibres take this direction. Their relative situation is internal.

2. External fibres, fewer than the preceding, which pass from the optic tract to the eye upon the same side.

3. Fibres situated on the posterior boundary of the commissure, which pass from one optic tract to the other and do not go to the eyes. These fibres are scanty and are sometimes wanting.

4. Fibres situated on the anterior border of the commissure, greater in number than the preceding, which pass from one eye to the other and which have no connection with the optic tracts.

FIG. 243.—*Diagram of the decussation of fibres at the optic commissure.*

The dotted lines show the four directions of the fibres.

The fibres of the optic tracts upon the two sides are connected with distinct portions of the retina. This fact is illustrated in cases of hemianopsia, which show that the decussating fibres have the following directions and distribution:

From the left side of the encephalon, fibres pass to the right eye, supplying the inner, or nasal mathematical half of the retina, from a vertical line passing through the macula lutea. Fibres also pass to the left eye, supplying the outer, or temporal half of the retina. The macula lutea, then, and not the point of entrance of the optic nerve, is in the true line of division of the retina.

With the exception of a few grayish filaments, the fibres of the optic tracts and the optic nerves are of the ordinary, medullated variety, and they present no differences in structure from the general cerebro-spinal nerves.

The optic commissure is covered with a fibrous membrane and is more resisting than the optic tracts. The optic nerves are rounded and are enclosed in a double sheath derived from the dura mater and the arachnoid. They pass into the orbit upon either side and penetrate the sclerotic, at the posterior, inferior and internal portion of the globe. As the nerves enter the globe, they lose their coverings from the dura mater and arachnoid. The sheath derived from the dura mater is adherent to the periosteum of the orbit, at the sphenoidal fissure, and when it reaches the globe, it fuses with the sclerotic coat. Just before the nerves penetrate the globe they each present a well-marked constriction. At the point of penetration there is a thin but strong membrane, presenting a number of perforations for the passage of the nervous filaments. This membrane, the lamina cribrosa, is in part derived from the sclerotic, and in part, from the coverings of the individual nerve-fibres, which lose their investing membranes at this point. In the interior of each eye there is a little, mammillated eminence, formed by the united fibres of the nerve. The retina, with which the optic nerve is connected, will be described as one of the coats of the eye.

In the centre of the optic nerve, is a minute canal, lined by fibrous tissue, in which are lodged the central artery of the retina and its corresponding vein, with a delicate nervous filament from the ophthalmic ganglion. The vessels penetrate the optic nerve $\frac{1}{3}$ to $\frac{3}{4}$ of an inch (8·5 to 19·1 mm.) behind the globe. The central canal does not exist behind these vessels.

*General Properties of the Optic Nerves.*—There is very little to be said regarding the general properties of the optic nerves, except that they are the only nerves capable of conveying to the cerebrum the special impressions of sight, and that they are not endowed with general sensibility.

That the optic nerves are the only nerves of sight, there can be no doubt. Their division or injury always involves loss or impairment of vision, directly corresponding with the extent of the lesion. It is important, however, to note that they are absolutely insensible to ordinary impressions. "We can, in a living animal, pinch, cauterize, cut, destroy in any way the optic nerve without giving rise to the slightest painful sensation; whether it be taken before or after its decussation, it seems completely insensible in its entire length" (Longet).

Not only are the optic nerve and retina insensible to pain, but their stimulation produces luminous impressions. This was stated in the remarkable paper, *Idea of a New Anatomy of the Brain*, printed by Charles Bell, in 1811. A few years later, Magendie, in operating for cataract, passed the needle to the bottom of the eye and irritated the retina, in two persons. The patients experienced no pain but merely an impression of flashes of light. The insensibility of the optic nerves has also been repeatedly noted in surgical operations in which the nerves have been exposed. If an electric current be passed through the optic nerves, a sensation of light is experienced. The same phenomenon is observed when the eyeball is pressed upon or contused, a fact which is sufficiently familiar.

### Physiological Anatomy of the Eyeball.

The eyeball is a spheroidal body, partially embedded in a cushion of fat in the orbit, protected by the surrounding bony structures and the eyelids, its surface bathed by the secretion of the lachrymal gland, and movable in various directions by the action of certain muscles. It is surrounded by a thin, serous sac, the capsule of Tenon, which exists in two layers. The outer layer lies next the fatty layer in which the globe is embedded, and the inner layer invests the sclerotic coat. When the axis of the eye is directed forward, the globe has the form of a sphere, in its posterior five-sixths, with the segment of a smaller sphere occupying its anterior sixth. The segment of the smaller sphere, bounded externally by the cornea, is more prominent than the rest of the surface.

The eyeball is made up of several coats enclosing certain refracting media. The external coat is the sclerotic, covering the posterior five-sixths of the globe, which is continuous with the cornea, covering the anterior sixth. This is a dense, opaque, fibrous membrane, for the protection of the inner coats and the contents of the globe. The cornea is dense, resisting and perfectly transparent. The muscles that move the globe of the eye are attached to the sclerotic coat.

Were it not for the prominence of the cornea, the eyeball would present very nearly the form of a perfect sphere, as will be seen by the following measurements of its various diameters; but the prominence of its anterior sixth gives the greatest diameter in the antero-posterior direction.

The form and dimensions of the globe are subject to considerable variations after death, by evaporation of the humors, emptying of vessels, etc., and there is no way in which the normal conditions can be restored. The most exact measurements are those made by Sappey. As an illustration of the post-mortem changes in the eye, Sappey has given comparative measurements made three hours and twenty-four hours after death, the results of which presented very considerable differences.

In measurements made by Sappey, one to four hours after death, of the eyes of twelve adult females and fourteen adult males, of different ages, the following mean results were obtained:

| SUBJECTS EXAMINED. | Diameters (inch, and mm. in parentheses). | | | |
|---|---|---|---|---|
| | Antero-posterior. | Transverse. | Vertical. | Oblique. |
| Mean of 12 females, 18 to 81 years of age. | 0·941 (23·9 mm.) | 0·911 (23·4 mm.) | 0·905 (23·0 mm.) | 0·937 (23·8 mm.) |
| Mean of 14 males, 20 to 79 years of age .. | 0·968 (24·6 mm.) | 0·941 (23·9 mm.) | 0·925 (23·5 mm.) | 0·949 (24·1 mm.) |

From these results it is seen that all the diameters are less in the female than in the male. The antero-posterior diameter is the greatest of all, and the vertical diameter is the shortest. The measurements at different ages, not cited in the table just given, show that the excess of the antero-posterior diameter over the others is diminished by age.

*Sclerotic Coat.*—The sclerotic is the dense, opaque, fibrous covering of the posterior five-sixths of the eyeball. Its thickness is different in different portions. At the point of penetration of the optic nerve, it measures $\frac{1}{25}$ of an inch (1 mm.) It is thinnest at the middle portion of the eye, measuring about $\frac{1}{50}$ of an inch (0·5 mm.), and is a little thicker again near the cornea. This membrane is composed chiefly of bundles of ordinary connective tissue. The fibres are slightly wavy, and are arranged in flattened bands, which are alternately longitudinal and transverse, giving the membrane a lamellated appearance, although it can not be separated into distinct layers. Mixed with these bands of connective-tissue fibres, are small fibres of elastic tissue. The vessels of the sclerotic are scanty. They are derived from the ciliary vessels and the vessels of the muscles of the eyeball. The tissue of the sclerotic yields gelatine on boiling.

*Cornea.*—The cornea is the transparent membrane which covers about the anterior sixth of the globe of the eye. As before remarked, this is the most prominent portion of the eyeball. It is in the form of a segment of a sphere, attached by its borders to the segment of the larger sphere formed by the sclerotic. The thickness of the cornea is about $\frac{1}{30}$ of an inch (0·8 mm.), in its central portion, and about $\frac{1}{25}$ of an inch (1 mm.) near its periphery. Its substance is composed of transparent fibres, arranged in incomplete layers, something like the layers of the sclerotic. It yields chondrine instead of gelatine on boiling.

Upon the external, or convex surface of the cornea, are several layers of delicate, transparent, nucleated epithelium. The most superficial cells are flattened, the middle cells are rounded, and the deepest cells are elongated and arranged perpendicularly. These cells become slightly opaque and whitish after death. Just beneath the epithelial covering of the cornea, is a very thin, transparent membrane, described by Bowman under the name of the "anterior elastic lamella." This membrane, with its cells, is a continuation of the conjunctiva.

The proper corneal membrane is composed of very pale, flattened bundles of fibres, interlacing with each other in every direction. Their arrangement is lamellated, although they can not be separated into complete and distinct layers. Between the bundles of fibres, lie a great number of stellate, anastomosing, connective-tissue corpuscles. In these cells and in the intervals between the fibres, there is a considerable quantity of transparent liquid. The fibres constituting the substance of the cornea are continuous with the fibrous structure of the sclerotic, from which they can not be separated by maceration At the margin of the cornea the opaque fibres of the sclerotic abruptly become transparent. The corneal substance is very tough, and it will resist a pressure sufficient to rupture the sclerotic.

Upon the posterior, or concave surface of the cornea, is the membrane of Descemet or of Demours. This is elastic, transparent, structureless, rather loosely attached, and covered with a single layer of regularly polygonal, nucleated epithelium. At the circumference of the cornea, a portion of this membrane passes to the anterior surface of the iris, in the form of a number of processes which constitute the ligamentum iridis pectinatum, a portion passes into the substance of the ciliary muscle, and a portion is continuous with the fibrous structure of the sclerotic.

In the adult the cornea is almost without blood-vessels, but in fœtal life it presents a rich plexus extending nearly to the centre. These disappear, however, before birth, leaving a very few delicate, looped vessels at the extreme edge.

In the cornea fine nerve-fibres terminate in the nuclei of the posterior layer of the epithelium of its convex surface. The cornea also contains lymph-spaces and the so-called "wandering cells." The surface of the cornea is exquisitely sensitive.

*Choroid Coat.*—Calling the sclerotic and the cornea the first coat of the eyeball, the second is the choroid, with the ciliary processes, the ciliary muscle and the iris. This was called by the older anatomists the uvea, a name which was later applied, sometimes to the entire iris, and sometimes to its posterior, or pigmentary layer. The choroid and ciliary processes will be described together as the second coat. The ciliary muscle and the iris will be described separately.

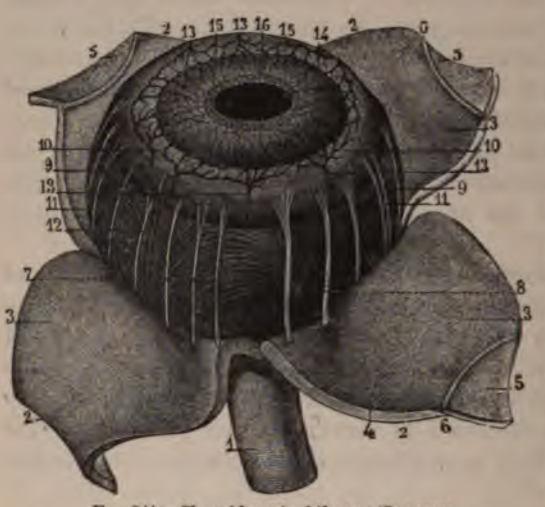

FIG. 244.—*Choroid coat of the eye* (Sappey).
1, optic nerve; 2, 2, 2, 2, 3, 3, 3, 4, sclerotic coat, divided and turned back to show the choroid; 5, 5, 5, 5, the cornea, divided into four portions and turned back; 6, 6, canal of Schlemm; 7, external surface of the choroid, traversed by the ciliary nerves and one of the long ciliary arteries; 8, central vessel, into which open the vasa vorticosa; 9, 9, 10, 10, choroid zone; 11, 11, ciliary nerves; 12, long ciliary artery; 13, 13, 13, 13, anterior ciliary arteries; 14, iris; 15, 15, vascular circle of the iris; 16, pupil.

The choroid is distinguished from the other coats of the eye by its dark color and its great vascularity. It occupies that portion of the eyeball corresponding to the sclerotic. It is perforated posteriorly by the optic nerve and is connected in front with the iris. It is very delicate in its structure and is composed of two or three distinct layers. Its thickness is $\frac{1}{85}$ to $\frac{1}{25}$ of an inch (0·3 to 1 mm.) Its thinnest portion is at about the middle of the eye. Posteriorly it is a little thicker. Its thickest portion is at its anterior border.

The external surface of the choroid is connected with the sclerotic by vessels and nerves (the long ciliary arteries and the ciliary nerves), and very loose, connective tissue. This is sometimes called the membrana fusca, although it can hardly be regarded as a distinct layer. It contains, in addition to blood-vessels, nerves and fibrous tissue, a few irregularly shaped pigment-cells.

The vascular layer of the choroid consists of arteries, veins and capillaries, arranged in a peculiar manner. The layer of capillary vessels, which is internal, is sometimes called the tunica Ruyschiana. The arteries, which are derived from the posterior short ciliary arteries and are connected with the capillary plexus, lie just beneath the pigmentary layer of the retina. The plexus of capillaries is closest at the posterior portion of the membrane. The veins are external to the other vessels. They are very abundant and are disposed in curves converging to four trunks. This arrangement gives the veins a very peculiar appearance, and they have been called the vasa vorticosa. The pigmentary portion is composed, over the greatest part of the choroid, of a single layer of regularly polygonal cells, somewhat flattened, measuring $\frac{1}{2000}$ to $\frac{1}{1500}$ of an inch (12 to 16 $\mu$) in diameter. These cells are filled with pigmentary granulations of uniform size, and they give to the membrane its characteristic dark-brown or chocolate color. The pigmentary granules in the cells are less abundant near their centre, where a clear nucleus can readily be observed. In the anterior portion of the membrane, in front of the anterior limit of the retina, the cells are smaller, more rounded, more completely filled with pigment, and present several layers. Beneath the layer of hexagonal pigment-cells, the intervascular spaces of the choroid are occupied by stellate pigment-cells. The cells next the layer of rods and cones are regarded as constituting the outer, or pigmentary layer of the retina. These cells send little, hair-like processes downward between the rods and cones.

*Ciliary Processes.*—The anterior portion of the choroid is arranged in the form of folds or plaits projecting internally, called the ciliary processes. The largest of these folds are about $\frac{1}{10}$ of an inch (2·5 mm.) in length. They are sixty to eighty in number. The larger folds are of nearly uniform size and are regularly arranged around the margin of the crystalline lens. Between these folds, which constitute about two-thirds of the entire number, are smaller folds, lying, without any regular alternation, between the larger. Within the folds, are received corresponding folds of the thick membrane, continuous anteriorly with the hyaloid membrane of the vitreous humor, called the zone of Zinn.

The ciliary processes present blood-vessels, which are somewhat larger than those of the rest of the choroid. The pigmentary cells are smaller and are arranged in several layers. The anterior border of the processes is free and contains little or no pigment.

*Ciliary Muscle.*—This muscle, formerly known as the ciliary ligament and now sometimes called the tensor of the choroid, is the agent for the accommodation of the eye to vision at different distances. Under this view, the ciliary muscle is an organ of great importance, and it is essential, in the study of accommodation, to have an exact idea of its relations to the coats of the eye and to the crystalline lens.

The form and situation of the ciliary muscle are as follows: It surrounds the anterior margin of the choroid, in the form of a ring about $\frac{1}{8}$ of an inch (3·2 mm.) wide and $\frac{1}{50}$ of an inch (0·5 mm.) in thickness at its thickest por-

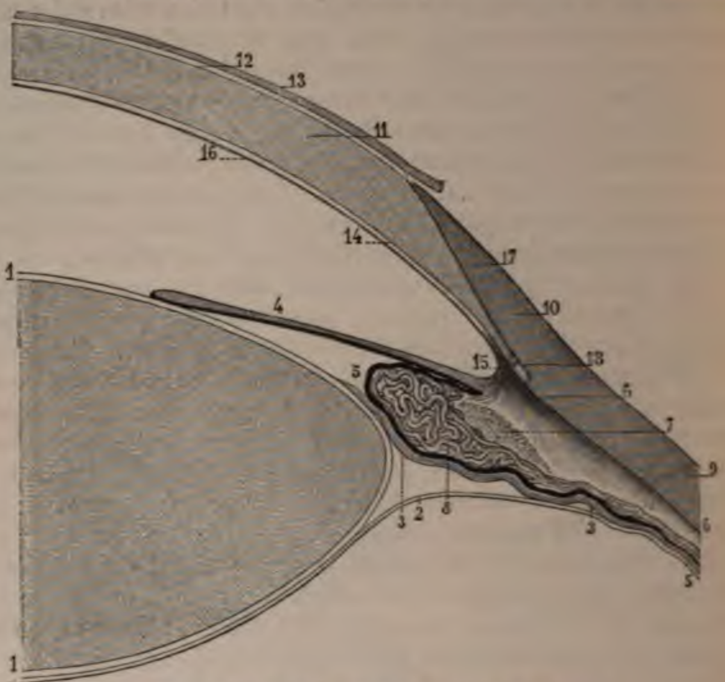


FIG. 245.—*Ciliary muscle; magnified 10 diameters* (Sappey).

1, 1, crystalline lens; 2, hyaloid membrane; 3, zone of Zinn; 4, iris; 5, 5, one of the ciliary processes; 6, 6, radiating fibres of the ciliary muscle; 7, section of the circular portion of the ciliary muscle; 8, venous plexus of the ciliary process; 9, 10, sclerotic coat; 11, 12, cornea; 13, epithelial layer of the cornea; 14, membrane of Descemet; 15, ligamentum iridis pectinatum; 16, epithelium of the membrane of Descemet; 17, union of the sclerotic coat with the cornea; 18, section of the canal of Schlemm.

tion, which is its anterior border. It becomes thinner from before backward, until its posterior border apparently fuses with the fibrous structure of the choroid. It is semi-transparent and of a grayish color. Its situation is just outside of the ciliary processes, these processes projecting in front of its anterior border, about $\frac{1}{25}$ of an inch (1 mm.). Regarding the anterior border of this muscle as its origin and the posterior border as its insertion, it arises in front, from the circular line of junction of the cornea and sclerotic, from the border of the membrane of Descemet, and the ligamentum iridis pectinatum. Its fibres, which are chiefly longitudinal, pass backward and are lost in the choroid, extending somewhat farther back than the anterior limit of the retina. In addition a net-work of circular muscular fibres has been described, lying over the anterior portion of the ciliary body, at the periphery of the iris, beneath the longitudinal fibres. Some of these fibres have an oblique direction.

The ciliary muscle is composed mainly of muscular fibres. These fibres, anatomically considered, belong to the non-striated variety. They are pale, present a number of oval, longitudinal nuclei, and have no striæ.

It is evident, from the arrangement of the fibres of the ciliary muscle, that its action must be to approximate the border of connection of the sclerotic and cornea and the circumference of the choroid, compressing the vitreous humor and relaxing the suspensory ligament of the crystalline lens. This action enables the lens to change its form, and it adapts the curvature of the lens to vision at different distances. The nerves of the ciliary muscle are derived from the long and the short ciliary.

*Iris.*—The iris corresponds to the diaphragm of optical instruments. It is a circular membrane, situated just in front of the crystalline lens, with a round perforation, the pupil, near its centre.

The attachment of the greater circumference of the iris is to the line of junction of the cornea and sclerotic, near the origin of the ciliary muscle, the latter passing backward to be inserted into the choroid, and the former passing directly over the crystalline lens. The diameter of the iris is about half an inch (12·5 mm.). The pupil is subject to considerable variations in size. When at its medium of dilatation, the diameter of the pupil is $\frac{1}{8}$ to $\frac{1}{6}$ of an inch (3·2 to 4·2 mm.). The pupillary orifice is not in the mathematical centre of the iris, but is situated a little toward the nasal side. The thickness of the iris is a little greater than that of the choroid, but it is unequal in different parts, the membrane being thinnest at its great circumference and its pupillary border, and thickest at about the junction of its inner third with the outer two-thirds. It slightly projects anteriorly and divides the space between the lens and the cornea into two chambers, anterior and posterior, the anterior chamber being much the larger. Taking advantage of a property of the crystalline lens, called fluorescence, which enables an observer, by concentrating upon it a blue light, to see the boundaries in the living eye, Helmholtz has demonstrated that the posterior surface of the iris and the anterior surface of the lens are actually in contact, except, perhaps, for a certain distance near the periphery of the iris. This being the case, the posterior chamber is very small and exists only near the margins of the lens and the iris.

The color of the iris is different in different individuals. Its anterior surface is generally very dark near the pupil and presents colored radiations toward its periphery. Its posterior surface is of a dark-purple color and is covered with pigmentary cells.

The entire iris presents three layers. The anterior layer is continuous with the membrane of the aqueous humor. At the great circumference, it presents little, fibrous prolongations, forming a delicate, dentated membrane, called the ligamentum iridis pectinatum. The membrane covering the general anterior surface of the iris is extremely thin and is covered by cells of tessellated epithelium. Just beneath this membrane are a number of irregularly shaped, pigmentary cells.

The posterior layer of the iris is very thin, easily detached from the middle layer, and contains a number of small cells rich in pigmentary granules. Some anatomists recognize this membrane only as the uvea.

The middle layer constitutes by far the greatest part of the substance of the iris. It is composed of connective tissue, muscular fibres of the non-striated variety, many blood-vessels, and probably nerve-terminations. Directly surrounding the pupil, forming a band about $\frac{1}{50}$ of an inch (0·5 mm.) in width, is a layer of non-striated muscular fibres, called the sphincter of the iris. The existence of these fibres is admitted by all anatomists. It is different, however, for the radiating muscular fibres. Most anatomists describe, in addition to the sphincter, non-striated fibres, which can be traced from near the great circumference of the iris almost to its pupillary border, lying both in front of and behind the circular fibres. A few observers deny that these fibres are muscular; but they recognize a thick, muscular layer surrounding the arteries of the iris. This is merely a question of observation; but the weight of anatomical authority is in favor of the existence of the radiating fibres, and their presence explains certain of the phenomena of dilatation of the iris which would otherwise be difficult to understand.

The blood-vessels of the iris are derived from the arteries of the choroid, from the long posterior ciliary and from the anterior ciliary arteries. The long ciliary arteries are two branches, running along the sides of the eyeball, between the sclerotic and choroid, to form finally a circle surrounding the iris. The anterior ciliary arteries are derived from the muscular branches of the ophthalmic. They penetrate the sclerotic, a little behind the iris, and join the long ciliary arteries, in the vascular circle. From this circle, the vessels branch and pass into the iris, to form a smaller arterial circle around the pupil. The veins from the iris empty into a circular sinus situated at the junction of the cornea with the sclerotic. This is sometimes spoken of as the circular venous sinus, or the canal of Schlemm.

The nerves of the iris are the long ciliary, from the fifth cranial, and the short ciliary, from the ophthalmic ganglion.

*Pupillary Membrane.*—At a certain period of fœtal life the pupil is closed by a membrane connected with the lesser circumference of the iris, called the pupillary membrane. This is not distinct during the first months; but between the third and the fourth months, it is readily seen. It is most distinct at the sixth month. The membrane is thin and transparent, and it completely separates the anterior from the posterior chamber of the eye. It is provided with vessels derived from the arteries of the iris, anastomosing with each other and turning back in the form of loops near the centre. At about the seventh month, it begins to give way at the centre, gradually atrophies, and scarcely a trace of it can be seen at birth.

*Retina.*—The retina is described by anatomists as the third tunic of the eye. It is closely connected with the optic nerve, and the most important structures entering into its composition are probably continuous with prolongations from the nerve-cells. This is the membrane endowed with the special sense of sight, the other structures in the eye being accessory.

If the sclerotic and choroid be removed from the eye under water, the retina is seen, in perfectly fresh specimens, in the form of a delicate, transparent membrane covering the posterior portion of the vitreous humor. A short time after death it becomes slightly opaline. It extends over the posterior portion of the eyeball, to a distance of about $\frac{1}{15}$ of an inch (1·7 mm.) behind the ciliary processes. When torn from its anterior attachment, it presents a finely serrated edge, called the ora serrata. This edge adheres very closely, by mutual interlacement of fibres, to the zone of Zinn. In the middle of the membrane, its thickness is about $\frac{1}{125}$ of an inch (200 $\mu$). It becomes thinner nearer the anterior margin, where it measures only about $\frac{1}{300}$ of an inch (80 $\mu$). Its external surface is in contact with the choroid, and its internal, with the hyaloid membrane of the vitreous humor.

The optic nerve penetrates the retina about $\frac{1}{8}$ of an inch (3·2 mm.) within and $\frac{1}{12}$ of an inch (2·1 mm.) below the antero-posterior axis of the globe, presenting at this point a small, rounded elevation upon the internal surface of the membrane, perforated in its centre for the passage of the central artery of the retina. At a point $\frac{1}{12}$ to $\frac{1}{8}$ of an inch (2·1 to 3·2 mm.) external to the point of penetration of the nerve, is an elliptic spot, its long diameter being horizontal, about $\frac{1}{8}$ of an inch (2·1 mm.) long and $\frac{1}{36}$ of an inch (0·7 mm.) broad, called the yellow spot of Sömmerring, or the macula lutea. In the centre of this spot, is a depression, called the fovea centralis. This depression is exactly in the axis of distinct vision. The yellow spot exists only in man and the quadrumana.

The structures in the retina which present the greatest physiological importance are the external layer, formed of rods and cones, the layer of nerve-cells, and the filaments which connect the rods and cones with the cells. These are the only anatomical elements of the retina, as far as is known, except the pigment cells, that are directly concerned in the reception of optical impressions, and they will be described rather minutely, while the intermediate layers will be considered more briefly.

Most anatomists recognize nine layers in the retina:

1. Layer of pigment-cells (already described in connection with the choroid).
2. Jacob's membrane, the bacillar membrane, or the layer of rods and cones.
3. The external granule-layer.
4. The inter-granule layer (cone-fibre plexus of Hulke).
5. The internal granule-layer.
6. The granular layer.
7. The layer of nerve-cells (ganglion-layer).
8. The expansion of the fibres of the optic nerve.
9. The limitary membrane.

The layer of rods and cones is composed of rods, or cylinders, extending through its entire thickness, closely packed, and giving to the external surface a regular, mosaic appearance; and between these, are a greater or less number of flask-shaped bodies, the cones. This layer is about $\frac{1}{330}$ of an inch (76 $\mu$) in thickness at the middle of the retina; $\frac{1}{400}$ of an inch (62 $\mu$), about midway between the centre and the periphery; and near the periphery, about $\frac{1}{450}$ of an inch (55 $\mu$). At the macula lutea the rods are wanting, and the layer is composed entirely of cones, which are here very much elongated.

Over the rest of the membrane the rods predominate, and the cones become less and less frequent toward the periphery.

The rods are regular cylinders, their length corresponding to the thickness of the layer, terminating above in truncated extremities, and below in points which are probably continuous with the filaments of connection with the nerve-cells. Their diameter is about $\frac{1}{12000}$ of an inch (2 $\mu$). They are clear, of rather a fatty lustre, soft and pliable, but somewhat brittle, and so alterable that they are with difficulty seen in a natural state. They should be examined in perfectly fresh preparations, moistened with liquid from the vitreous humor or with serum. When perfectly fresh it is difficult to make out any thing but an entirely homogeneous structure; but shortly after death each rod seems to be divided by a delicate line into an outer and an inner segment, the outer being a little the longer. At the upper extremity of the inner segment, is a hemispherical body, with its convexity presenting inward, called the lentiform body (*linsenförmiger Körper*). The entire inner segment is somewhat granular, and it often presents a granular nucleus at its inner extremity. The outer segment apparently differs in its constitution from the inner segment and is not similarly affected by reagents. Treated with dilute acetic acid, the outer segment becomes broken up transversely into thin disks.


FIG. 246.—*Rods of the retina* (Schultze).

From the monkey.—*A.* Rods, after maceration in iodized serum, the outer segment (*b*) truncated, the inner segment (*a*) coagulated, granular, and somewhat swollen: *c*, filament of the rods; *d*, nucleus.

*B.* Rods from the frog: 1. Fresh, magnified 500 diameters; *a*, inner segment; *b*, outer segment; *c*, lentiform body; *d*, nucleus. 2. Treated with dilute acetic acid and broken up into plates.

The cones are probably of the same constitution as the rods, but that portion called the inner segment is pyriform. The straight portion above (the outer segment) is sometimes called the cone-rod. The entire cones are about half the length of the rods and occupy the inner portion of the layer. The outer segment is in its constitution precisely like the outer segment of the rods. The inner segment is slightly granular and contains a nucleus. The cones are connected below with filaments passing into the deeper layers of the retina. The arrangement of the rods and cones is seen in Fig. 247, which shows the different layers of the retina.

At the fovea centralis, Jacob's membrane is composed entirely of elongated cones, with no rods. These are slightly increased in thickness at the macula lutea, but are diminished again in thickness, by about one-half, at the fovea centralis. At the fovea the optic nerve-fibres are wanting; and the ganglion-cells, which exist in a single layer over other portions of the retina, here present six to eight layers, except at the very centre, where there are but three layers. Of the layers between the cones and the ganglion cells, the external granule-layer and the inter-granule layer (cone-fibre plexus) remain, in the fovea, while the internal granule-layer and the granular layer are wanting. At the fovea, indeed, those elements of the retina which may be garded as purely accessory disappear, leaving only the structures that are ncerned directly in the reception of visual impressions.

The external granule-layer is composed of large granules, looking like lls, which are each nearly filled with a single nucleus. These are connected ith the filaments from the rods and cones. They are rounded or ovoid d measure from $\frac{1}{13000}$ to $\frac{1}{6000}$ of an inch (2 to 4 $\mu$) in diameter. The ter-granule layer (cone-fibre plexus) is composed apparently of minute brillæ and a few nuclei. The internal granule-layer is composed of cells early like those of the external granule-layer, but a little larger, and prob-

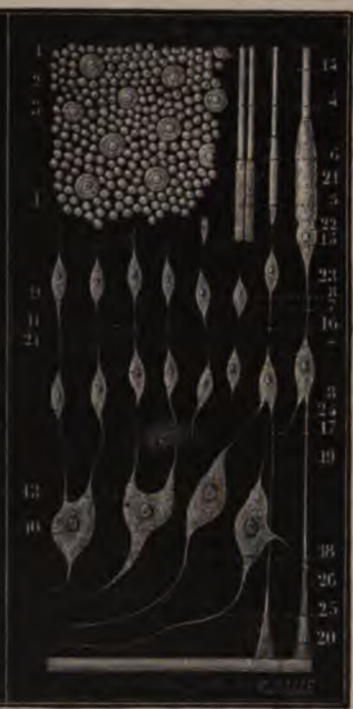

FIG. 247.—*Vertical section of the retina* (H. Müller).

FIG. 248.—*Connection of the rods and cones of the retina with the nervous elements* (Sappey).

G. 247.—1, 1, layer of rods and cones; 2, rods; 3, cones; 4, 4, 5, 6, external granule-layer; 7, inter-granule layer (cone-fibre plexus); 8, internal granule-layer; 9, 10, finely granular, gray layer; 11, layer of nerve-cells; 12, 12, 12, 12, 14, 14, fibres of the optic nerve; 13, membrana limitans. (The pigmentary layer is not shown in this figure.)

G. 248.—1, 1, 2, 3, rods and cones, front view; 4, 5, 6, rods, side view; 7, 7, 8, 8, cells of the external and internal granule-layers; 9, cell, connected by a filament with subjacent cells; 10, 13, nerve-cells connected with cells of the granule-layers; 11, 21, filaments connecting cells of the external and internal granule-layers (12 is not in the figure); 14, 15, 16, 17, 18, 19, 20, 22, 23, 24, 25, 26, a rod and a cone, connected with the cells of the granule-layers, with the nerve-cells and with the nerve-fibres.

ly connected with the filaments of the rods and cones. The granular yer is situated next the layer of ganglion-cells.

The layer of ganglion-cells is composed of multipolar nerve-cells, measuring $\frac{1}{000}$ to $\frac{1}{750}$ of an inch (8 to 32 $\mu$) in diameter. In the centre of the retina, the macula lutea, the cells present eight layers, and they diminish to a ngle layer near the periphery. The smaller cells are situated near the centre, and the larger, near the periphery. Each cell sends off several filaments (two to twenty-five), probably going to the layer of rods and cones, and a single filament which becomes continuous with one of the filaments of the optic nerve.

The layer formed by the expansion of the optic nerve is composed of pale, transparent nerve-fibres, $\frac{1}{50000}$ to $\frac{1}{25000}$ of an inch (0·5 to 1 $\mu$) in diameter. These do not require special description.

The limitary membrane is a delicate structure, with fine striæ and nuclei, composed of connective-tissue elements. It is about $\frac{1}{25000}$ of an inch (1 $\mu$) in thickness. From this membrane, connective-tissue elements are sent into the various layers of the retina, where they form a framework for the support of the other structures.

The retina becomes progressively thinner from the centre to the periphery. The granular layers and the nervous layers rapidly disappear in the anterior half of the membrane.

The following is the probable mode of connection between the rods and cones and the ganglion-cells: The filaments from the bases of the rods and cones pass inward, presenting in their course the corpuscles which have been described in the granule-layers, and finally become, as is thought, directly continuous with the poles of the ganglion-cells. The cells send filaments to the layer formed by the expansion of the optic nerve, which are continuous with the nerve-fibres. This arrangement is shown in Fig. 248.

The following description of the blood-vessels of the retina, with Fig. 249, was furnished by Loring:

"The arteries and veins of the retina are subdivisions of the arteria and vena centralis. The larger branches run in the nerve-fibre layer and are immediately beneath the limitary membrane. The vessels lie so superficially that in a cross-section examined with the microscope, they are seen to project above the general level of the retina, toward the vitreous humor. While the large vessels are in the plane of the inner surface of the retina, the smaller branches penetrate the substance of the retina, to the inter-granule layer. They do not extend, however, as far as the external granule-layer and the layer of rods and cones. These two layers, therefore, have no blood-vessels.

"The ramifications of the vessels present a beautifully arborescent appearance when seen with the ophthalmoscope. The manner in which the vessels are distributed and the way in which the circulation is carried on can be better understood by a study of Fig. 249 than by any detailed description. The figure represents the ophthalmoscopic appearance of a normal eye in young, adult life. The darker vessels are the veins, and the lighter vessels, the arteries. The dotted oval line is diagrammatic and marks the position and extent of the macula lutea. It is seen that this oval space contains a number of fine vascular twigs which, coming from above and below, extend toward the spot in the centre of the oval which marks the position of the fovea centralis. In opposition, then, to the general opinion, which is that the macula lutea has no blood-vessels, it is the spot of all others in the retina which is most abundantly supplied with minute vascular branches. These vessels can be distinctly seen even with the ophthalmoscope; and microscopical examination shows that the capillary plexus in the macula lutea is closer and richer than in any other part of the retina."

FIG. 249.—*Blood-vessels of the retina; magnified 7½ diameters* (Loring).

The arteries of the retina send branches to the periphery, where they supply a wide plexus of very small capillaries in the ora serrata. These capillaries empty into an incomplete venous circle, branches from which pass back by the sides of the arteries, to the vena centralis.

*Crystalline Lens.*—The crystalline is a double-convex lens, which is perfectly transparent and very elastic. Its action in the refraction of the rays of light is analogous to that of convex lenses in optical instruments. It is situated behind the pupil, in what is called the hyaloid fossa of the vitreous humor, which is exactly moulded to its posterior convexity. In the fœtus the capsule of the lens receives a branch from the arteria centralis, but it is non-vascular in the adult. The anterior convexity of the lens is just behind the iris, and its borders are in relation with what is known as the suspensory ligament. The convexities do not present regular curves, and they are so subject to variations after death that the measurements, post mortem, are of little value. During life, however, they have been measured very exactly in the various conditions of accommodation. The diameters of the lens in the adult are about ⅓ of an inch (8·5 mm.) transversely and ¼ of an inch (6·4 mm.) antero-posteriorly. The convexity is greater on its posterior than on its anterior surface. In fœtal life the convexities of the lens are greater than in the adult and its structure is much softer. In old age the convexities are diminished and the lens becomes harder and less elastic. The substance of the lens is made up of layers of fibres of different degrees of density, and the whole is enveloped in a delicate membrane, called the capsule.

The capsule of the lens is a thin, transparent membrane, which is very elastic. This membrane generally is from $\frac{1}{2500}$ to $\frac{1}{1500}$ of an inch (10 to 17 $\mu$) thick; but it is very thin at the periphery, measuring here only $\frac{1}{6000}$ of an inch (4 $\mu$). Its thickness is increased in old age. The anterior portion of the capsule is lined on its inner surface with a layer of exceedingly delicate, nucleated epithelial cells. The posterior half of the capsule has no epithelial lining. The cells are regularly polygonal, measuring $\frac{1}{2000}$ to $\frac{1}{1250}$ of an inch (12 to 20 $\mu$) in diameter, with large, round nuclei. After death, they are said to break down into a liquid, known as the liquid of Morgagni, though by some this liquid is supposed to be exuded from the substance of the lens. At all events, the cells disappear soon after death.

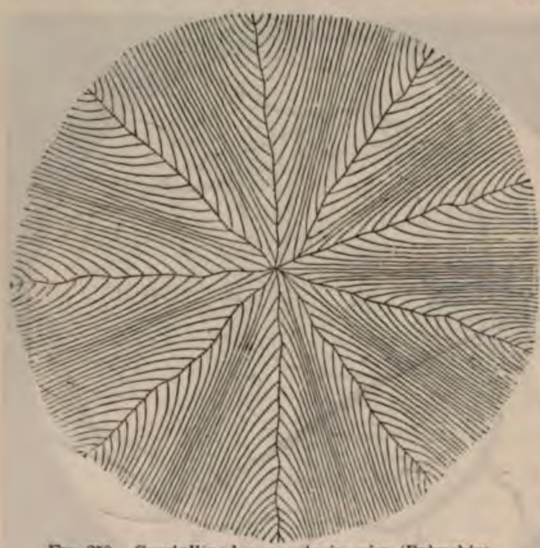

FIG. 250.—*Crystalline lens; anterior view* (Babuchin).

If the lens be viewed entire with a low magnifying power, it presents upon either of its surfaces, a star with nine to sixteen radiations extending from the centre to about half or two-thirds of the distance to the periphery. The stars seen upon the two surfaces are not coincident, the rays of one being situated between the rays of the other. In the fœtus the stars are more simple, presenting only three radiations upon either surface. These stars are not fibrous, like the rest of the lens, but are composed of a homogeneous substance, which extends, also, between the fibres.

FIG. 251.—*Section of the crystalline lens* (Babuchin).

The greatest part of the substance of the lens is composed of very delicate, soft and pliable fibres, which are transparent, but perfectly distinct. These fibres are flattened, six-sided prisms, closely packed together, so that their transverse section presents a regularly tesselated appearance. They are $\frac{1}{5000}$ to $\frac{1}{2500}$ of an inch (5 to 10 $\mu$) broad, and $\frac{1}{13000}$ to $\frac{1}{9000}$ of an inch (2 to 3 $\mu$) in thickness. Their flat surfaces are parallel with the surface of the lens. The direction of the fibres is from the centre and from the rays of the stellate figures to the periphery, where they turn and pass to the star upon the opposite side. The outer layers of fibres near the equator, or circumference of the lens, contain exceedingly distinct, oval nuclei, with one or two nucleoli. These become smaller in passing more deeply into the substance of the lens, and gradually they disappear.

The regular arrangement of the fibres of the lens makes it possible to separate its substance into laminæ, which have been compared by anatomists to the layers of an onion; but this separation is entirely artificial, and the number of apparent layers depends upon the dexterity of the manipulator. It is to be noted, however, that the external portions of the lens are soft, even gelatinous, and that the central layers are much harder, forming a sort of central kernel, or nucleus.

The lens is composed of a nitrogenized substance, called crystalline, combined with various inorganic salts. One of the constant constituents of this body is cholesterine. In an examination of four fresh crystalline lenses of the ox, cholesterine was found in the proportion of 0·907 of a part per 1,000 (Flint). In some cases of cataract cholesterine exists in the lens in a crystalline form; but under normal conditions it is united with the other constituents.

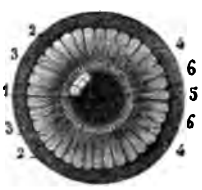


FIG. 252.—*Zone of Zinn* (Sappey).
1, crystalline lens; 2, 2, vitreous humor; 3, 3, zone of Zinn; 4, 4, posterior portion of the zone of Zinn, thrown into folds; 5, 6, 6, anterior and middle portions of the zone of Zinn.

*Suspensory Ligament of the Lens* (*Zone of Zinn*).—The vitreous humor occupies about the posterior two-thirds of the globe, and is enveloped in a delicate capsule, called the hyaloid membrane. In the region of the ora serrata of the retina, this membrane divides into two layers. The posterior layer lines the depression in the vitreous humor into which the lens is received. The anterior layer passes forward toward the lens and divides into two secondary layers, one of which passes forward, to become continuous with the anterior portion of the capsule of the lens, while the other passes to the posterior surface of the lens, to become continuous with this portion of its capsule. The anterior of these layers is corrugated or thrown into folds which correspond with the ciliary processes, with which it is in contact. This corrugated portion is called the zone of Zinn. The two layers thus surround the lens and are properly called its suspensory ligament. As the two layers of the suspensory ligament separate at a certain distance from the lens, one passing to the anterior and the other to the posterior portion of the capsule, there remains a triangular canal, about $\frac{1}{10}$ of an inch (2·5 mm.) wide, surrounding the border of the lens, called the canal of Petit. Under natural conditions the walls of this canal are nearly in apposition, and it contains a very small quantity of clear liquid.

The membrane forming the suspensory ligament is composed of pale, longitudinal and transverse fibres of rather a peculiar appearance, which are much less affected by acetic acid than the ordinary fibres of connective tissue.

*Aqueous Humor.*—The space bounded in front by the cornea, posteriorly, by the crystalline lens and the anterior face of its suspensory ligament, and at its circumference, by the tips of the ciliary processes, is known as the aqueous chamber. This contains a clear liquid called the aqueous humor. The iris separates this space into two divisions, which communicate with each other through the pupil; viz., the anterior chamber, situated between the anterior face of the iris and the cornea, and the posterior chamber, between the posterior face of the iris and the crystalline. It is evident, from the position of the iris, that the anterior chamber is much the larger; and, indeed, the posterior surface of the iris and the anterior surface of the lens are in contact, except, perhaps, near their periphery or when the iris is very much dilated. The liquid filling the chambers of the eye is rapidly reproduced after it has been evacuated, as occurs in many surgical operations upon the eye.

The aqueous humor is colorless and transparent, faintly alkaline, of a specific gravity of about 1005, and with the same index of refraction as that of the cornea and the vitreous humor. It contains a small quantity of an albuminoid matter, but it is not rendered turbid by heat or other agents which coagulate albumen. Various inorganic salts (the chlorides, sulphates, phosphates and carbonates) exist in small proportions in this liquid. It also contains traces of urea and glucose.

The anterior and posterior chambers of the eye are regarded as lymph-spaces communicating with the lymphatics of the conjunctiva, cornea, iris and ciliary processes. In addition a lymph-space is described as existing between the choroid and the sclerotic. This space is supposed to communicate with a perivascular canal-system around the vasa vorticosa, and through these vessels, with the space between the capsule of Tenon and the sclerotic (Schwalbe). The latter is connected with lymph-channels which surround the optic nerve (Key and Retzius).

*Vitreous Humor.*—The vitreous humor is a clear, glassy substance, occupying about the posterior two-thirds of the globe. It is enveloped in a delicate, structureless capsule, called the hyaloid membrane, which is about $\frac{1}{6000}$ of an inch (4 $\mu$) in thickness. This membrane adheres rather strongly to the limitary membrane of the retina. In front, at the ora serrata, the hyaloid membrane is thickened and becomes continuous with the suspensory ligament of the lens.

The vitreous humor itself is gelatinous, of feeble consistence and slightly alkaline in its reaction, with a specific gravity of about 1005. Upon section there oozes from it a watery and slightly mucilaginous liquid. This humor is not affected by heat or alcohol, but it is coagulated by certain mineral salts, especially lead acetate. When thus solidified it presents regular layers, like the white of an egg boiled in its shell; but these are artificial. In the embryon the vitreous humor is divided into a number of little cavities and contains cells and leucocytes. It is also penetrated by a branch from the central artery of the retina, which passes through its centre, to ramify upon the posterior surface of the crystalline lens. This structure, however, is not found in the adult, the vitreous humor being then entirely without blood-vessels. The vitreous humor is divided into compartments formed by delicate membranes radiating from the point of penetration of the optic nerve to the anterior boundary where the hyaloid membrane is in contact with the capsule of the lens. In this way the humor is divided up, something like the half of an orange, by about one hundred and eighty membranous processes of extreme delicacy, which do not interfere with its transparency.

### Summary of the Anatomy of the Globe of the Eye.

This summary is intended simply to indicate the relations and the physiological importance of the various parts of the eye, in connection with Fig. 253.

The eyeball is nearly spherical in its posterior five-sixths, its anterior sixth

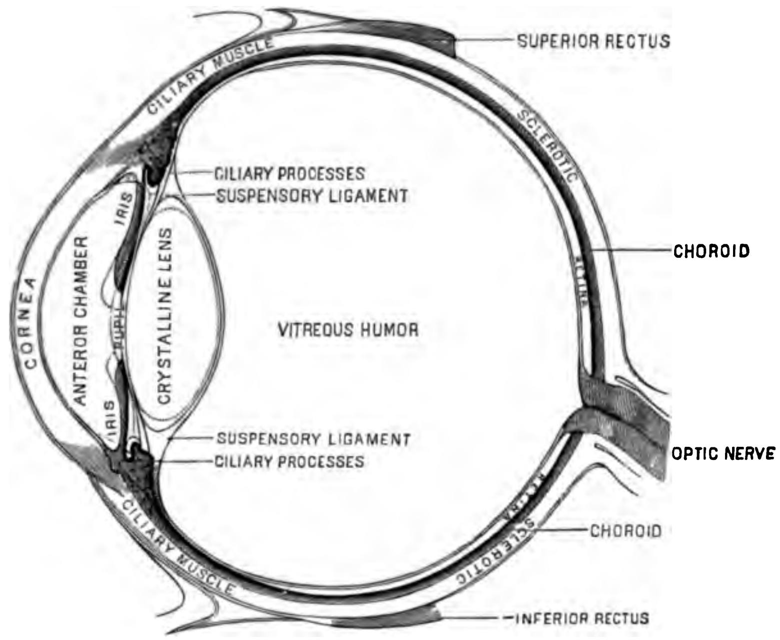


Fig. 253.—*Section of the human eye.*

being formed of the segment of a smaller sphere, which is slightly projecting. It presents the following parts, indicated in the figure.

The sclerotic; a dense, fibrous membrane, chiefly for the protection of the more delicate structures of the globe, and giving attachment to the muscles which move the eyeball. Attached to the sclerotic are the tendons of the recti and the oblique muscles.

The cornea; a transparent structure, forming the anterior, projecting sixth of the globe; dense and resisting, allowing, however, the passage of light; covered, on its convex surface, with several layers of transparent epithelial cells.

The choroid coat; lining the sclerotic and extending only as far forward as the cornea; connected with the sclerotic by loose, connective tissue, in which ramify blood-vessels and nerves, and presenting an external, vascular layer and an internal, pigmentary layer, which latter gives its characteristic dark-brown color.

The ciliary processes; peculiar folds of the choroid, which form its anterior border and which embrace the folds of the suspensory ligament of the lens.

The ciliary muscle; situated just outside of the ciliary processes, arising from the circular line of junction of the sclerotic with the cornea, passing over the ciliary processes, and becoming continuous with the fibrous tissue of the choroid. The action of this muscle is to tighten the choroid over the vitreous humor and to relax the ciliary processes and the suspensory ligament of the lens, when the lens, by virtue of its elasticity, becomes more convex. This action is shown by the dotted lines in the figure.

The iris; dividing the space in front of the lens into two chambers occupied by the aqueous humor. The anterior chamber is much the larger. The iris, in its central portion surrounding the pupil, is in contact with the lens. Its circumference is just in front of the line of origin of the ciliary muscle.

The retina; a delicate, transparent membrane, lining the choroid and extending to about $\frac{1}{15}$ of an inch (1·7 mm.) behind the ciliary processes, the anterior margin forming the ora serrata. The optic nerve penetrates the retina a little internal to and below the antero-posterior axis of the globe. The layer of rods and cones is situated next the pigmentary layer, which is external. Internal to the layer of rods and cones, are the four granular layers; next, the layer of nerve-cells; next, the expansion of the fibres of the optic nerve; and next, in apposition with the hyaloid membrane of the vitreous humor, is the limitary membrane.

The crystalline lens; elastic, transparent, enveloped in its capsule and surrounded by the suspensory ligament.

The suspensory ligament; the anterior layer connected with the anterior portion of the capsule of the lens, and the posterior, with the posterior portion of the capsule. The folded portion of this ligament, which is received between the folds of the ciliary processes, is called the zone of Zinn. The triangular canal between the anterior and the posterior layers of the suspensory ligament and surrounding the equator of the lens is called the canal of Petit.

The vitreous humor; enveloped in the hyaloid membrane, which membrane is continuous in front, with the suspensory ligament of the lens.

### Refraction in the Eye.

In applying some of the elementary laws of refraction of light to the transparent media of the eye, it is necessary to bear in mind certain general facts with regard to vision, that have as yet been referred to either very briefly or not at all.

The eye is not a perfect optical instrument, looking at it from a purely physical point of view. This statement, however, should not be understood as implying that the arrangement of the parts is not such as to adapt them perfectly to their uses in connection with the proper appreciation of visual impressions. By physical tests it can be demonstrated that the eye is not entirely achromatic; but in ordinary vision the dispersion of colors is not appreciated. There is but a single point in the retina, the fovea centralis, where vision is absolutely distinct; and it is upon this point that images are made to fall when the eye is directed toward any particular object.

The refracting apparatus is not exactly centred, a condition so essential to the satisfactory performance of perfect optical instruments. For example, in a compound microscope or a telescope, the centres of the different lenses entering into the construction of the instrument are all situated in a straight line. Were the eye a perfect optical instrument, the line of vision would coincide exactly with the axis of the cornea; but this is not the case. The visual line—a line drawn from an object to its image on the fovea centralis—deviates from the axis of the cornea, in normal eyes, to the nasal side. The visual line, therefore, forms an angle with the axis of the cornea. This is known as the angle alpha. This deviation of the visual line from the mathematical centre of the eye is observed both in the horizontal and in the vertical planes. The horizontal deviation varies by two to eight degrees (Schuerman), and the vertical, by one to three degrees (Mandelstamm). Of course this want of exact centring of the optical apparatus, in normal eyes, does not practically affect distinct vision; for when the eyes are directed toward any object, this object is brought in the line of the visual axis; but the angle apha is an important element to be taken into account in various mathematical calculations connected with the physics of the eye.

The area of distinct vision is quite restricted; but were it larger, it is probable that the mind would become confused by the extent and variety of the impressions, and that it would not be so easy to observe minute details and fix the attention upon small objects.

Although certain objects are seen with absolute distinctness only in a restricted field, the angle of vision is very wide, and rays of light are admitted from an area equal to nearly the half of a sphere. Such a provision is eminently adapted to visual requirements. The eyes are directed to a particular point and a certain object is seen distinctly, with the advantage of an image in the two eyes, exactly at the points of distinct vision; the rays coming from without the area of distinct vision are received upon different portions of the surface of the retina and produce an impression more or less indistinct, not interfering with the observation of the particular object to which the attention is for the moment directed; but even while looking intently at any object, the attention may be attracted by another object of an unusual character, which might, for example, convey an idea of danger, and the point of distinct vision can be turned in its direction. Thus, while but few objects are seen distinctly at one time, the area of indistinct vision is very large; and the attention may readily be directed to unexpected or unusual objects that come within any portion of the field of view. The small extent of the area of distinct vision, especially for near objects, may readily be appreciated in watching a person who is attentively reading a book, when the eyes will be seen to follow the lines from one side of the page to the other with perfect regularity. When it is considered that in addition to these qualities, which are not possible in artificial optical instruments, the eye may be accommodated at will to vision at different distances, and that there is correct appreciation of form, etc., by the use of the two eyes, it is evident that the visual organ gains rather than loses in comparison with the most perfect instruments that have been constructed.

*Certain Laws of Refraction, Dispersion etc., bearing upon the Physiology of Vision.*—Physiologists have little to do with the theory of light, except as regards the modifications of luminous rays in passing through the refracting media of the eye. It will be sufficient to state that nearly all physicists of the present day agree in accepting what is known as the theory of undulation, rejecting the emission-theory proposed by Newton. It is necessary to the theory of undulation to assume that all space and all transparent bodies are permeated with what has been called a luminiferous ether; and that light is propagated by a vibration or an undulation of this hypothetical substance. This theory assimilates light to sound, in the mechanism of its propagation; but in sound the waves are supposed to be longitudinal, or to follow the line of propagation, while in light the particles are supposed to vibrate transversely, or at right angles to the line of propagation. It must be remembered, however, that the undulatory theory of sound is capable of positive demonstration, and that the propagation of sound by waves can take place only through ponderable matter, the vibrations of which can always be observed; but the theory of luminous vibrations involves the existence of an hypothetical ether. It is possible, indeed, that scientific facts may in the future render the existence of such an ether improbable or its supposition unnecessary; but at present the theory of luminous undulation seems to be in accord with the optical phenomena that have thus far been recognized.

The different calculations of physicists with regard to the velocity of light have been remarkably uniform in their results. The lowest calculations put it at about 185,000 miles (297,725 kilometres) in a second, and the highest, at about 195,000 miles (313,818 kilometres). The rate of propagation is usually assumed to be about 192,000 miles (309,000 kilometres).

The intensity of light is in proportion to the amplitude of the vibrations. The intensity diminishes as the distance of the luminous body increases, and is in inverse ratio to the square of the distance.

In the theory of the colors into which pure white light may be decomposed by prisms, it is assumed to be a matter of demonstration that the waves of the different colors of the solar spectrum are not of the same length. The decomposition of light is produced by differences in the refrangibility of the different colored rays as they pass through a medium denser than the air.

The analysis of white light into the different colors of the spectrum shows that it is compound; and by synthesis, the colored rays may be brought together, producing white light. Colors may be obtained by decomposition of light by transparent bodies, the different colored rays being refracted, or bent, by a prism, at different angles. It is not in this way, however, that the colors of different objects are produced. Certain objects have the property of reflecting the rays of light. A perfectly smooth, polished surface, like a mirror, may reflect all of the rays; and the object then has no color, only the reflected light being appreciated by the eye. Certain other objects do not reflect all of the rays of light, some of them being lost to view, or absorbed. When an object absorbs all of the rays, it has no color and is called black. When an object absorbs the rays equally and reflects a portion of these rays without decomposition, it is gray or white. There are many objects, however, that decompose white light, absorbing certain rays of the spectrum and reflecting others. The rays not absorbed, but returned to the eye by reflection, give color to the object. Thus, if an object absorb all of the rays of the spectrum except the red, the red rays strike the eye, and the color of the object is red. So it is with objects of different shades, the colors of which are given simply by the unabsorbed rays.

A mixture of different colors in certain proportions will result in white. Two colors, which, when mixed, result in white, are called complementary. The following colors of the spectrum bear such a relation to each other: Red and greenish-blue; orange and cyanogen-blue; yellow and indigo-blue; greenish-yellow and violet.

The fact that impressions made upon the retina persist for an appreciable length of time affords an illustration of the law of complementary colors. If a disk, presenting divisions with two complementary colors, be made to revolve so rapidly that the impressions made by the two colors are blended, the resulting color is white.

*Refraction by Lenses.*—A ray of light is an imaginary pencil, so small as to present but a single line; and the light admitted to the interior of the eye by the pupil is supposed to consist of an infinite number of such rays. In studying the physiology of vision, it is important to recognize the laws of refraction of rays by transparent bodies bounded by curved surfaces, with particular reference to the action of the crystalline lens.

The action of a double-convex lens, like the crystalline, in the refraction of light, may readily be understood by a simple application of the well known laws of refraction by prisms. A ray of light falling upon the side of a prism at an angle is deviated toward a line perpendicular to the surface of the prism. As the ray passes from the prism to the air, it is again refracted, but the deviation is then from the perpendicular of the second surface of the prism. In passing through a prism, therefore, the pencil of light is bent, or refracted, toward the base.

A circle is equivalent to a polygon with an infinite number of sides. A regular, double-convex lens is a transparent body bounded by segments of a sphere. Theoretically a double-convex lens may be assumed to be composed of an infinite number of sections of prisms (Fig. 254, I.), or to make the comparison with prisms more striking, although less accurate, the lens may be assumed to be composed of prisms (Fig. 254, II., Weinhold).

If these prisms or sections of prisms be infinitely small, so that the surface of each receives but a single infinitely small pencil of light, these pencils will be refracted toward the bases of the prisms, and different rays of light from all points of an object may be brought to an infinite number of foci, all these foci, for a plane object, being in the same plane. If the number of sections be equal on every side of the centre of the lens, the bases looking toward the axis of the lens, the rays of light will cross at a certain point, and the image formed by the lens will be inverted. This is illustrated in Fig.

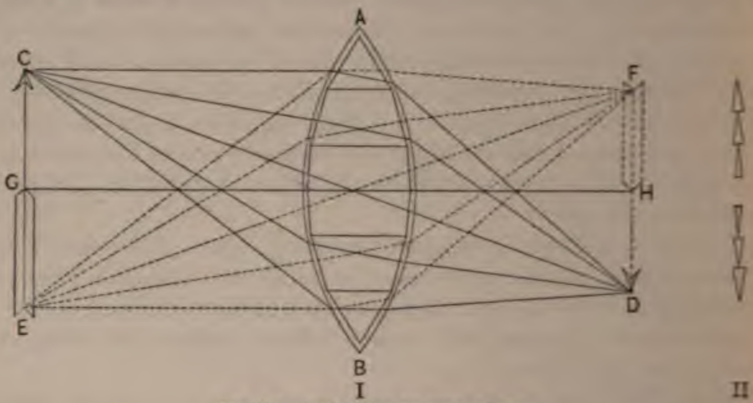


FIG. 254.—*Refraction by convex lenses.*

254, which represents a section of a lens theoretically dissected into six sections of prisms.

If the lens A B (Fig. 254) be assumed to be free from what is known as spherical aberration, the rays from the point C will be refracted, and brought to a focus at the point D. In the same way the rays from E will be brought to a focus at F, the two sets of rays crossing before they reach their focal points. The same is true for all the rays from every point in the image C E, which strike the lens at an angle, but the ray G H, which is perpendicular to the lens, is not deviated. The rays of light are refracted in this way by the cornea and by the crystalline lens. The retina is normally at such a distance from the lens that the rays are brought to a focus exactly at its surface. Inasmuch as the rays cross each other before they reach the retina, the image is always inverted.

Supposing the crystalline lens to be free from spherical and chromatic aberration, the formation of a perfect image depends upon the following conditions:

The object must be at a certain distance from the lens. If the object be too near, the rays, as they strike the lens, are too divergent and are brought to a focus beyond the plane F H D, or behind the retina; and as a consequence the image is confused. In optical instruments the adjustment is made for objects at different distances by moving the lens itself. In the eye, however, the adjustment is effected by increasing or diminishing the curvatures of the lens, so that the rays are always brought to a focus at the visual surface of the retina. The faculty of thus changing the curvatures of the crystalline lens is called accommodation. This power, however, is restricted within certain well defined limits.

In some individuals the antero-posterior diameter of the eye is too long, and the rays, for most objects, come to a focus before they reach the retina. This defect may be remedied by placing the object very near the eye, so as to increase the divergence of the rays as they strike the crystalline. Such persons are said to be near-sighted (myopic), and objects are seen distinctly, only when very near the eye. This defect may be remedied for distant objects, by placing concave lenses before the eyes, by which the rays falling upon the crystalline are diverged. The opposite condition, in which the antero-posterior diameter is too short (hypermetropia), is such that the rays are brought to a focus behind the retina. This is corrected by converging the rays of incidence, by placing convex lenses before the eyes. In old age the crystalline lens becomes flattened, its elasticity is diminished and the power of accommodation is lessened; conditions which also tend to bring the rays to a focus behind the retina. This condition is called presbyopia. To render near vision—as in reading—distinct, objects are placed farther from the eye than under normal conditions. The defect may be remedied, as in hypermetropia, by placing convex lenses before the eyes, by which the rays are converged before they fall upon the crystalline lens.

The mechanism of accommodation will be fully considered in connection with the physiology of the crystalline lens; and at present it is sufficient to state that in looking at distant objects, the rays as they fall upon the lens are nearly parallel. The lens is then in repose, or "indolent." It is only when an effort is made to see near objects distinctly, that the agents of accommodation are called into action; and then, very slight changes in the curvature of the lens are sufficient to bring the rays to a focus exactly on the visual surface of the retina.

*Spherical, Monochromatic Aberration.*—In a convex lens in which the surfaces are segments of a sphere, the rays of light from any object are not converged to a uniform focus, and the production of an absolutely distinct image is impossible. For example, if the crystalline lens had regular curvatures, the rays refracted by its peripheral portion would be brought to a focus in front of the retina; the focus of the rays converged by the lens near its centre would be behind the retina; a few, only, of the rays would have their focus at the retina itself; and as a consequence, the image would appear confused. This is illustrated in imperfectly corrected lenses, and is called spherical aberration. It is also called monochromatic aberration, because it is to be distinguished from an aberration which involves decomposition of light into the colors of the spectrum. If an object be examined under the microscope with an imperfectly corrected objective, it is evident that the field of view is not uniform, and that there is a different focal adjustment for the central and the peripheral portions of the lens. In the construction of optical instruments, this difficulty may be in part corrected if the rays of light be cut off from the periphery of the lens, by a diaphragm, which is an opaque screen with a circular perforation allowing the rays to pass to a restricted portion of the lens, near its centre. The iris corresponds to the diaphragm of optical instruments, and it corrects the spherical aberration of the crystalline in part, by eliminating a portion of the rays that would otherwise fall upon its peripheral portion. This correction, however, is not sufficient for high magnifying powers; and it is only by the more or less perfect correction of this kind of aberration by other means, that powerful lenses have been rendered available in optics.

The spherical aberration of lenses which diverge the rays of light is precisely opposite to the aberration of converging lenses. In a compound lens, therefore, it is possible to fulfill the conditions necessary to the convergence of all the incident rays to a focus on a uniform plane, so that the image produced behind the lens is not distorted. Given, for example, a double-convex lens, by which the rays are brought to innumerable focal points situated in different planes. The fact that but a few of these focal points are in the plane of the retina renders the image indistinct. If a concave or a plano-concave lens be placed in front of this convex lens, which will diverge the rays more or less, the inequality of the divergence by different portions of the second lens will have the following effect: As the angle of divergence gradually increases from the centre toward the periphery, the rays near the periphery, which are most powerfully converged by the convex lens, will be most widely diverged by the peripheral portion of the concave lens; so that if the opposite curvatures be accurately adjusted, the aberrant rays may be blended. It is evident that if all the rays were equally converged by the convex lens and equally diverged by the concave lens, the action of the latter would be simply to elongate the focal distance; and it is equally evident that if the aberration of the one be exactly opposite to the aberration of the other, there will be perfect correction. Mechanical art has not effected correction of every portion of very powerful convex lenses in this way; but by a combination of lenses and diaphragms together, highly magnified images, nearly perfect, have been produced. Lenses in which spherical aberration has been corrected are called aplanatic.

It is evident that for distinct vision at different distances, the crystalline lens must be nearly free from spherical aberration. This is not effected by a combination of lenses, as in ordinary optical instruments, but by the curvatures of the lens itself, and by certain differences in the consistence of different portions of the lens, which will be fully considered hereafter.

*Chromatic Aberration.*—A refracting medium does not act equally upon the different colored rays into which pure white light may be decomposed; in other words, as the pure ray falling upon the inclined surface of a glass prism is bent, it is decomposed into the colors of the spectrum. As a convex lens is practically composed of an infinite number of prisms, the same effect would be expected. Indeed, a simple convex lens, even if the spherical aberration be corrected, always produces more or less decomposition of light.

The image formed by such a lens will consequently be colored; and this defect in simple lenses is called chromatic aberration. At the same time it is evident that the centre of the different rays from an object will be composed of all the colors of the spectrum combined, producing the effect of white light; but at the borders the different colors will be separate and distinct, and an image produced by a simple convex lens will thus be surrounded by a circle of colors, like a rainbow.

In prisms the chromatic dispersion may be corrected by allowing the colored rays from one prism to fall upon a second prism, which is inverted, so that the colors will be brought together and produce white light. Two prisms thus applied to each other constitute, in fact, a flat plate of glass, and the rays of light pass without deviation. If this law be applied to lenses, it is evident that the dispersive power of a convex lens may be exactly opposite to that of a concave lens. By the convex lens the colored rays are separated by convergence and cross each other; and in the concave lens the colored rays are diverged in the opposite direction. If, then, a convex be combined with a concave lens, the white light decomposed by the one will be recomposed by the other, and the chromatic aberration will thus be corrected; but in using a convex and a concave lens composed of the same material, the convergence by the one will be neutralized by the divergence of the other, and there will be no amplification of the object. Newton supposed that dispersion, or decomposition of light, by lenses was always in exact proportion to refraction, so that it would be impossible to correct chromatic aberration and retain magnifying power; but it has been ascertained that there are great differences in the dispersive power of different kinds of glass, without corresponding differences in refraction. This discovery rendered it possible to construct achromatic lenses (Dollond, 1757). According to Ganot, Hall was the first to make achromatic lenses, in 1753, but his discovery was not published.

In the construction of modern optical instruments, the chromatic aberration is corrected, with a certain diminution in the amplification, by cementing together lenses made of different material, as of flint-glass and crown-glass. Flint-glass has a much greater dispersive power than crown-glass. If, therefore, a convex lens of crown-glass be combined with a concave or plano-concave lens of flint-glass, the chromatic aberration of the convex lens may be corrected by a concave lens with a curvature which will reduce the magnifying power about one-half. A compound lens, with the spherical aberration of the convex element corrected by the curvature of a concave lens, and the chromatic aberration corrected in part by the curvature, and in part by the superior refractive power of flint-glass over crown-glass, will produce a perfect image.

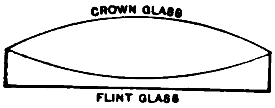

FIG. 235.—*Achromatic lens.*

Although the eye is not absolutely achromatic, the dispersion of light is not sufficient to interfere with distinct vision; but the chromatic aberration is practically corrected in the crystalline lens, probably by differences in the consistence and in the refractive power of its different layers.

### Formation of Images in the Eye.

It is necessary only to call to mind the general arrangement of the different structures in the eye and to apply the simple laws of refraction, in order to comprehend precisely how images are formed upon the retina.

The eye corresponds to a camera obscura. Its interior is lined with a dark, pigmentary membrane (the choroid), the immediate action of which is to prevent the confusion of images by internal reflection. The rays of light are admitted through a circular opening (the pupil), the size of which is regulated by the movements of the iris. The pupil is contracted when the light striking the eye is intense, and is dilated as the quantity of light is diminished. In the accommodation of the eye, the pupil is dilated for distant objects and contracted for near objects; for in looking at near objects, the aberrations of sphericity and achromatism in the lens are more marked, and the peripheral portion is cut off by the action of this movable diaphragm, thus aiding the correction. The rays of light from an object pass through the cornea, the aqueous humor, the crystalline lens and the vitreous humor, and they are refracted with so little spherical and chromatic aberration, that the image formed upon the retina is practically perfect. The layer of rods and cones of the retina is the only portion of the eye endowed directly with special sensibility, the impressions of light being conveyed to the brain by the optic nerves. This layer is situated next the pigmentary layer of the choroid, but the other layers of the retina, through which the light passes to reach the rods and cones, are perfectly transparent.

It has been shown that the rods and cones are the only structures capable of directly receiving visual impressions, by the following experiment, first made by Purkinje: With a convex lens of short focus, an intense light is concentrated on the sclerotic, at a point as far as possible removed from the cornea. This passes through the translucent coverings of the eye at this point, and the image of the light reaches the retina. In then looking at a dark surface, the field of vision presents a reddish-yellow illumination, with a dark, arborescent appearance produced by the shadows of the large retinal vessels; and as the lens is moved slightly, the shadows of the vessels move with it. Without going elaborately into the mechanism of this phenomenon, it is sufficient to state that Heinrich Müller has arrived at a mathematical demonstration that the shadows of the vessels are formed upon the layer of rods and cones, and that this layer alone is capable of receiving impressions of light. His explanation is generally accepted and is regarded as positive proof of the peculiar sensibility of this portion of the retina.

Theoretically, an illuminated object placed in the angle of vision would form upon the retina an image, diminished in size and inverted. This fact is capable of demonstration by means of the ophthalmoscope; as with this instrument the retina and the images formed upon it may be seen during life.

All parts of the retina, except the point of entrance of the optic nerve, are sensitive to light; and the arrangement of the cornea and pupil is such, that the field of vision is, at the least estimate, equal to the half of a sphere.

If a ray of light fall upon the border of the cornea, at a right angle to the axis of the eye, it is refracted by its surface and will pass through the pupil to the opposite border of the retina. Above and below, the circle of vision is cut off by the overhanging arch of the orbit and the malar prominence; but externally the field is free. With the two eyes, therefore, the lateral field of vision must be equal to at least one hundred and eighty degrees. It is easy to demonstrate, however, by the ophthalmoscope, as well as by taking cognizance of the impressions made by objects far removed from the axis of distinct vision, that images formed upon the lateral and peripheral portions of the retina are confused and imperfect. One has a knowledge of the presence and an indefinite idea of the general form of large objects situated outside of the area of distinct vision; but when it is desired to note such objects exactly, the eyeball is turned by muscular effort, so as to bring them at or very near the axis of the globe. This fact, with what is known of the mechanism of refraction by the cornea and lens, makes it evident that the area of the retina, upon which images are formed with perfect distinctness, is quite restricted. A moment's reflection is sufficient to convince any one that in order to see any object distinctly, it is necessary to bring the axis of the eye to bear upon it directly.

In examining the bottom of the eye with the ophthalmoscope, the yellow spot, with the fovea centralis, can be seen, free from large blood-vessels, and composed chiefly of those elements of the retina which are sensitive to light. If at the same time, an image for which the eye is perfectly adjusted be observed, it will be seen that this image is perfect only at the fovea centralis; and if the object be removed from the axis of vision, there is a confused image upon the retina, removed from the fovea, at the same time that the subject is conscious of indistinct vision. In the words of Helmholtz, "It is only in the immediate vicinity of the ocular axis that the retinal image possesses entire distinctness; beyond this, the contours are less defined. It is in part for this reason that in general we see distinctly in the field of vision, only the point that we fix. All the others are seen vaguely. This lack of distinctness in indirect vision, in addition, depends also upon diminished sensibility of the retina: at a slight distance from the fixed point, the distinctness of vision has diminished much more than the objective distinctness of retinal images."

At the point of penetration of the optic nerve, the retina is insensible to luminous impressions; or at least, its sensibility is here so obtuse as to be entirely inadequate for the purposes of vision. This point is called the punctum cæcum; and its want of sensibility was demonstrated many years ago (1668) by Mariotte. The classical experiment by which this important fact was ascertained is generally known as Mariotte's experiment. The following account is quoted *verbatim:*

"I fasten'd on an obscure Wall about the hight of my Eye, a small round paper, to serve me for a fixed point of Vision; and I fastened such an other on the side thereof towards my right hand, at the distance of about 2. foot; but somewhat lower than the first, to the end that it might strike the *Optick*

*Nerve* of my Right Eye, whilst I kept my Left shut. Then I plac'd myself over against the First paper, and drew back by little and little, keeping my Right Eye fixt and very steddy upon the same; and being about 10. foot distant, the second paper totally disappear'd."

In this experiment the rays of light from the paper which has disappeared from view are received upon the punctum cæcum, at the point of entrance of the optic nerve. If the observer withdraw himself still farther, the second circle will reappear, as the rays are removed from the punctum cæcum. With the ophthalmoscope, the point of penetration of the optic nerve may readily be seen in the living eye. If the image of a flame be directed upon this point, the sensation of light is either not perceived or it is very faint and indefinite, and it is then probably due to diffusion to other portions of the retina.

The relative sensibility of different portions of the retina has been measured by Volkmann and has been found to be, in an inverse ratio, equal to about the square of the distance from the axis of most perfect vision. This observer calculated the distance between the sensitive elements of the retina at which he supposed that two parallel lines would appear as one. In the axis of vision, the distance was 0·00029 inch (7·366 $\mu$), and at a deviation inward of 8°, it was 0·03186 inch (809·244 $\mu$), a diminution of acuteness of more than a hundred times.

*Visual Purple and Visual Yellow, and Accommodation of the Eye for Different Degrees of Illumination.*—The outer segments of the rods of the retina sometimes present a peculiar red or purple color, which disappears after ten or twelve seconds of exposure to light. This was first observed by Boll (1876) in the retinæ of frogs that had been kept for a certain time in the dark. From his preliminary researches, Boll concluded that this coloration of the retina exists only during life and persists but a few moments after death; that it is constantly destroyed during life by the action of light and reappears in the dark; and finally that it plays an important part in the act of vision. Kühne and others have since confirmed and extended the original observations of Boll; and the visual purple (rhodopsine) has been noted in the mammalia and in man. It has been extracted from the retinæ of frogs and dissolved in a five-per-cent. solution of crystallized ox-gall, still presenting in solution its remarkable sensitiveness to light (Ayres). Finally it has been found possible to fix images of simple objects, such as strips of black paper pasted upon a plate of ground glass, upon the retina, by a process very like that of photography.

The visual purple is produced by the cells of the pigmentary layer of the retina and from them is absorbed by the outer segments of the rods. It is not present in any part of the cones and does not exist, therefore, in the area of distinct vision, at the fovea centralis. The rapid disappearance of the color under the influence of actinic rays of light renders it necessary to examine the retina under a non-actinic (monochromatic) sodium-flame (Ayres). When thus examined and gradually exposed to actinic rays, the color quickly fades into a yellow and finally disappears, being restored, however, in the dark.

If the choroid and the pigmentary layer of the retina be removed, the rods are bleached, and the color is restored in the dark when the choroid is replaced. In the eye of the frog, kept in the dark, the hair-like processes which extend from the pigmentary layer of the retina downward between the rods and cones are retracted, and the pigment is then contained chiefly in the cells themselves. After prolonged exposure of the retina to light, these processes, loaded with pigment, extend between the cones as far as the limitary membrane (Kühne).

The fact that visual purple has never been found in the fovea centralis is opposed to the theory that its existence is directly essential to distinct vision; nevertheless, certain phenomena observed in passing from a bright light to comparative obscurity, and the reverse, show that the purple has, at least, an important indirect action. In passing from the dark to bright light, the eye is dazzled and distinct vision is difficult. It may be assumed that this is due to unusual general sensitiveness of the retina to light, on account of the excessive quantity of visual purple which has accumulated in the dark, and that distinct vision is restored when the retina is bleached to a yellow, which seems to be the most favorable condition for the exact appreciation of visual impressions, under full illumination. On the other hand, it requires time for the eye to become accustomed to a dim light; and during this time the yellow is changing to purple. These changes in the color of the retina have been actually observed (Ayres). Investigations of the absorption-spectra of the purple and yellow have shown that the purple allows the actinic rays to pass perfectly, while the yellow completely absorbs these rays (Kühne). The existence of visual purple seems to be most favorable to the imperfect and shadowy vision which occurs under dim illumination, when the exact appreciation of minute details is impossible. In the condition known as night-blindness, it is probable that the visual purple has become exhausted beyond the possibility of prompt restoration such as is normal; and persons so affected can not see at night, although minute vision under a bright light may not be affected. In certain cases of this kind, the normal conditions may be restored by a few days' seclusion in the dark. What is called functional night-blindness frequently occurs in sailors during long, tropical voyages, and is due to the excessive action of diffused light upon the retina. "That the affection is local, is shown by the fact that darkening one eye, with a bandage, during the day, has been found to restore its sight enough for the ensuing night's watch on board ship, the unprotected eye remaining as bad as ever" (Nettleship).

The change of the visual purple to yellow is readily effected, but the farther change to white is slower and more difficult. Conversely, the change from white to yellow is slow and the change from yellow to purple is comparatively prompt. One use of the colors purple and yellow seems to be to accommodate the retina for vision under different degrees of illumination. The purple adapts the eye to a feeble illumination, and the yellow, to a full illumination. This being the case, it is manifestly proper to speak of a visual yellow (Kühne) as well as of visual purple.

That the accommodation of the eye to different degrees of illumination is due to the changes in the colors produced by the pigmentary layer of the retina and not to different degrees of dilatation of the pupil, is shown by the fact that a person does not see better in the dark when the pupil has been dilated by atropine (Loring). In a very dim light there is no possibility of exact accommodation for near objects, which, when small, can not be seen distinctly; and the contraction of the pupil which attends accommodation for near vision does not occur. It is possible that under dim illumination, parts outside of the fovea, which are insensible to vision under a bright light, receive visual impressions. Under these conditions the pupil is dilated and rays impinge on portions of the retina not used in direct vision. A natural extension of this idea would confine distinct vision and the appreciation of minute details to the action of the fovea centralis, in which there is no visual purple, other parts of the retina, under full illumination, not being used. To express this in a few words, the fovea centralis is used by day, and the adjacent parts of the retina, by night.

### Mechanism of Refraction in the Eye.

An object that is seen reflects rays from every point of its surface, to the cornea. If the object be near, the rays from each and every point are divergent as they strike the eye. Rays from distant objects are practically parallel. It is evident that the refraction for diverging rays must be greater than for parallel rays, as a necessity of distinct vision; in other words, the eye must be accommodated for vision at different distances. Leaving, however, the mechanism of accommodation for future consideration, it may be stated simply that the important agents in refraction in the eye are the surfaces of the cornea and the crystalline lens. Calculations have shown that the index of refraction of the aqueous humor is sensibly the same as that of the substance of the cornea, so that practically the refraction is the same as if the cornea and the aqueous humor were one and the same substance. The index of refraction of the vitreous humor is practically the same as that of the aqueous humor, both being about equal to the index of refraction of pure water. Refraction by the crystalline lens, however, is more complex in its mechanism; depending first, upon the curvatures of its two surfaces, and again, upon the differences in the consistence of different portions of its substance. In view of these facts, the conditions of refraction in the eye in distinct vision may be simplified by assuming the following arrangement:

The cornea presents a convex surface upon which the rays of light are received. At a certain distance behind its anterior border, is the crystalline, a double convex lens, corrected sufficiently for all practical purposes, both for spherical and chromatic aberration. This lens is practically suspended in a liquid with an index of refraction equal to that of pure water, as both the aqueous humor in front and the vitreous humor behind have the same refractive power. Behind the lens, in its axis and exactly in the plane upon which the rays of light are brought to a focus by the action of the cornea and the lens, is the fovea centralis, which is the centre of distinct vision. The anatomical elements of the fovea are capable of receiving visual impressions, which are conveyed to the brain by the optic nerves. All impressions made upon other portions of the retina are comparatively indistinct; and the point of entrance of the optic nerve is insensible to light. Inasmuch as the punctum cæcum is situated in either eye upon the nasal side of the retina, in normal vision, rays from the same object can not fall upon both blind points at the same time. Thus, in binocular vision, the insensibility of the punctum cæcum does not interfere with sight; and the movements of the globe prevent any notable interference in vision, even with one eye. The sclerotic coat is for the protection of its contents and for the insertion of muscles. The iris has an action similar to that of the diaphragm in optical instruments. The suspensory ligament of the lens, the ciliary body, and the ciliary muscle, are for the fixation of the lens and its accommodation for distinct vision at different distances. The choroid is a dark membrane, for the absorption of light, preventing confusion of vision from reflection within the eye.

Refraction by the cornea is effected simply by its external surface. The rays of light from a distant point are deviated by its convexity so that, if they were not again refracted by the crystalline lens, they would be brought to a focus at a point situated about $\frac{4}{10}$ of an inch (10 mm.) behind the retina. Without the crystalline lens, therefore, distinct, unaided vision generally is impossible, although the sensation of light is appreciated. In cases of extraction of the lens for cataract (aphakia), the crystalline is supplied by a convex lens placed before the eye.

The rays of light, refracted by the anterior surface of the cornea, are received upon the anterior surface of the crystalline lens, by which they are still farther refracted. Passing through the substance of the lens, they undergo certain modifications in refraction, dependent upon the differences in the various strata of the lens. These modifications have not been accurately calculated; but it is sufficient to state that they contribute to the accuracy of the formation of the retinal image and to the production of an image practically free from chromatic dispersion. As the rays pass out of the crystalline lens, they are again refracted by its posterior curvature and are brought to a focus at the point of distinct vision.

The rays from all points of an object distinctly seen are brought to a focus, if the accommodation of the lens be correct, upon a restricted surface in the macula lutea; but the rays from different points cross each other before they reach the retina, and the image is inverted.

Calculating the curvatures of the refracting surfaces in the eye and the indices of refraction of its transparent media, it has been pretty clearly shown, by mathematical formulæ, that the eye—viewed simply as an optical instrument, and not practically, as the organ of vision—presents a certain degree of spherical and chromatic aberration; but these calculations are not very important in a purely physiological consideration of the sense of sight.

In most calculations of the size of images, the positions of conjugate foci, etc., in normal and abnormal eyes, a schematic eye reduced by Donders, after the example of Listing, is regarded as sufficiently exact for all practical purposes. This simple scheme represents the eye as reduced to a single refracting surface, the cornea, and a single liquid assumed to have an index of refraction equal to that of pure water. The distance between what are called the two nodal points and between the two principal points of the dioptric system of the eye is so small, amounting to hardly $\frac{1}{100}$ of an inch (0·254 mm.), that it can be neglected. In this simple eye, there is assumed to be a radius of curvature of the cornea of about $\frac{1}{5}$ of an inch (5 mm.) and a single optical centre situated $\frac{1}{5}$ of an inch (5 mm.) back of the cornea, the "principal point" being in the cornea, in the axis of vision. The posterior focal distance, that is, the focus, at the bottom of the eye, for rays that are parallel in the air, is about $\frac{4}{5}$ of an inch (20 mm.). The anterior focal distance, that is, for rays parallel in the vitreous humor, is about $\frac{3}{5}$ of an inch (15 mm.). The measurements in this simple schematic eye can easily be remembered and used in calculations.

### Astigmatism.

In the normal human eye the visual line does not coincide exactly with the mathematical axis; but there is still another normal deviation from mathematical exactness in the refraction of rays by the cornea and the crystalline lens, which is of considerable importance. If two threads, crossing each other at right angles in the same plane, be placed before the eyes, one of these threads being vertical, and the other, horizontal, when the optical apparatus is adjusted so that one line is seen with perfect distinctness, the other is not well defined. In other words, when the eye is accommodated for the vertical thread, the horizontal thread is indistinct, and *vice versâ*. If the horizontal line be seen distinctly, in order to see the vertical line without modifying the accommodation, it must be removed to a greater distance. This depends chiefly upon a difference in the vertical and the horizontal curvatures of the cornea, so that the horizontal meridian has a focus slightly different from the focus of the vertical meridian. A condition opposite to that observed in the cornea usually exists in the crystalline lens; that is, the difference which exists between the curvatures of the lens in the vertical and the horizontal meridians is such that the deepest curvature in the lens is situated in the meridian of the shallowest curvature of the cornea. In this way, in normal eyes, the aberration of the lens has a tendency to correct the aberration in the cornea; but this correction is incomplete, and there still remains, in all degrees of accommodation, a certain difference in vision, as regards vertical and horizontal lines.

The condition just described is known under the name of normal, regular astigmatism; but the aberration is not sufficiently great to interfere with distinct vision. The degree of regular astigmatism presents normal variations in different eyes. In some eyes there is no astigmatism; but this is rare. According to Donders, if the astigmatism amount to $\frac{1}{40}$ or more, it is to be considered abnormal; which simply means that beyond this point the aberration interferes with distinct vision.

From the simple definition of regular astigmatism, it is evident that this condition and the degree to which it exists may easily be determined by noting the differences in the foci for vertical and horizontal lines, and it may be exactly corrected by the application of cylindrical glasses of proper curvature. Indeed, the curvature of a cylindrical glass which will enable a person to distinguish vertical and horizontal lines with perfect distinctness at the same time, is an exact indication of the degree of aberration. Regular astigmatism, such as just described, may be so exaggerated as to interfere very seriously with vision, when it becomes abnormal. This kind of aberration, however, which is dependent upon an abnormal condition of the cornea, is remediable by the use of properly adjusted, cylindrical glasses.

Irregular astigmatism, excluding cases of pathological deformation, opaque spots etc., in the cornea, depends upon irregularity in the different sectors of the crystalline lens. Instead of a simple and regular aberration, consisting in a difference between the depth of the vertical and the horizontal curvatures of the cornea and lens, there are irregular variations in the curvatures of different sectors of the lens. As a consequence of this, when the irregularities are very great, there is impairment of the sharpness of vision. The circles of diffusion, which are regular in normal vision, become irregularly radiated, and single points appear multiple, an irregularity described under the name of polyopia monocularis. Accurate observations have shown that this condition exists to a very moderate degree in normal eyes; but it is so slight as not to interfere with ordinary vision. In what is called normal, irregular astigmatism, the irregularity depends entirely upon the crystalline lens. If a card with a very small opening be placed before the eye and be moved in front of the lens, so that the pencil of light falls successively upon different sectors, it can be shown that the focal distance is different for different portions. The radiating lines of light observed in looking at remote, luminous points, as the fixed stars, are produced by this irregularity in the curvatures of the different sectors of the lens.

While regular astigmatism, both normal and abnormal, may be perfectly corrected by placing cylindrical glasses before the eyes, it is impossible, in the great majority of cases, to construct glasses which will remedy what has been called irregular astigmatism.

### Movements of the Iris.

There are two physiological conditions under which the size of the pupil is modified: The first of these depends upon the degree of illumination to which the eye is exposed. When the illumination is dim, the pupil is widely dilated. When the eye is exposed to a bright light, the retina is protected by contraction of the iris. The muscular action by which the iris is contracted is characteristic of the smooth muscular fibres, as can be readily seen by exposing an eye, in which the pupil is dilated, to a bright light. Contraction does not take place instantly, but an appreciable interval elapses after the exposure, and a more or less gradual diminution in the size of the pupil is observed. This is seen both in solar and in artificial light. The second of these conditions depends indirectly upon the voluntary action of muscles.

The effort of converging the axes of the eyes, by looking at a very near object, contracts the pupils; and accommodation of the eye for near objects produces the same effect, even when the eyes are not converged. This action will be fully considered under the head of accommodation.

*Direct Action of Light upon the Iris.*—The variations in the size of the pupil under different physiological conditions are effected almost exclusively through the nervous system, either by reflex action from variations in the intensity of light, or by a direct influence, as in accommodation for distances; but it is nevertheless true that the muscular tissue of the iris will respond directly to the stimulus of light. Harless noted, in subjects dead of various diseases, five to thirty hours after death, that the iris contracted under the stimulus of light; and he regarded this as probably due to direct action upon its muscular tissue. It is not reflex, for the reason that the irritability of the nerves in warm-blooded animals disappears certainly in twenty hours after death. The experiments of Harless were made upon the two eyes, one being exposed to the light, while the other was closed. The contraction, however, took place very slowly, requiring an exposure of several hours. This mode of contraction is very different from the action of the iris during life, but it is precisely like the contraction observed after division of the motor oculi communis, which is slow and gradual and depends upon the direct action of light upon the muscular fibres.

*Action of the Nervous System upon the Iris.*—This subject, as far as it relates to the third pair, has been considered in connection with the physiology of these nerves; and it is unnecessary to refer again in detail to the experiments which have already been cited. The reflex phenomena observed are sufficiently distinct. When light is admitted to the retina, the pupil contracts, and the same result follows mechanical irritation of the optic nerves. When the third pair of nerves has been divided, no such reflex phenomena are observed. It is well known, also, that division of the third nerves in the lower animals or their paralysis in the human subject produces permanent dilatation of the pupil, the iris responding, only in the slow and gradual manner already indicated, to the direct action of light.

Taking all the experimental facts into consideration, it is certain that the third nerve has an important influence upon the iris. Filaments from the ophthalmic ganglion animate the circular fibres, or sphincter, and these filaments are derived from the third cranial nerve. If this nerve be divided, the iris becomes permanently dilated and is immovable, except that it responds very slowly to the direct action of light. The reflex action by which the pupil is contracted under the stimulus of light operates through the third nerve, and no such action can take place after this nerve has been divided. In view of these facts, there can be no doubt with regard to the nervous action upon the sphincter of the pupil, this muscle being animated exclusively by filaments from the motor oculi communis, coming through the ophthalmic ganglion.

Most anatomists admit the existence of radiating muscular fibres in the iris, the action of which is antagonistic to the circular fibres, and which dilate the pupil. That these fibres are subjected to nervous influence, is rendered certain by experiments upon the sympathetic system. There can be no doubt that the action of the sympathetic upon the pupil is directly antagonistic to that of the third pair, the former presiding over the radiating muscular fibres; and the only question to determine is the course taken by the sympathetic filaments to the iris. Experiments on the influence of the fifth pair upon the pupil have been somewhat contradictory in different animals. In rabbits section of this nerve in the cranial cavity produces contraction of the pupil; but in dogs and cats the same operation produces dilatation. In the human subject, of course, it is impossible to determine this point by direct experiment; and the varying results obtained in observations upon different animals probably depend upon differences in the anatomical relations of the nerves. It is probable, however, that the filaments of the sympathetic which animate the radiating fibres join the fifth nerve near the ganglion of Gasser, and from this nerve pass to the iris.

There seem to be two distinct nerve-centres corresponding to the two sets of nerves which regulate the movements of the iris. One of these centres presides over the reflex contractions of the iris, and the other is the centre of origin of the nervous influence through which the pupil is dilated.

The mechanism of reflex contraction of the iris under the stimulus of light is sufficiently simple. An impression is made upon the retina, which is conveyed by the optic nerves to the centre, and in obedience to this impression, the sphincter of the iris contracts. If the optic nerves be divided, so that the impression can not be conveyed to the centre, or if the third nerve be divided, no movements of the iris can take place. The centres which preside over the reflex phenomena of contraction of the pupil are situated in the medulla oblongata. The action of these centres is crossed in animals in which the decussation of the optic nerves is complete. In man the axes of both eyes are habitually brought to bear upon objects, and it is well known that there is a physiological unity in the action of the two eyes in ordinary vision. It has been observed that when one eye only is exposed to light, the pupil becoming contracted under this stimulus, the pupil of the other eye also contracts. There is, indeed, a direct contraction and dilatation of the pupil of the eye which is exposed to the light, and an indirect, or "consensual" movement of the iris upon the opposite side. The consensual contraction occurs about $\frac{3}{8}$ of a second later than the direct action, and the consensual dilatation, about $\frac{1}{2}$ of a second later (Donders).

Budge and Waller have shown that the filaments of the sympathetic which produce dilatation of the pupil take their origin from the spinal cord. In the spinal cord, between the sixth cervical and the second thoracic nerves, is the inferior cilio-spinal centre. When the spinal cord is stimulated in this situation, both pupils become dilated. If the cord be divided longitudinally and the two halves be separated from each other by a glass plate, stimulation of the right half produces dilatation of the right pupil, and *vice versâ*. This does not occur when the sympathetic in the neck has been divided. In addition to the inferior cilio-spinal centre, there is a superior centre, which is in communication with the superior cervical ganglion and is situated near the sublingual nerve. The influence of this centre over the pupil can not be demonstrated by direct stimulation, because it is too near the origin of the fifth, irritation of which affects the iris; but it is shown by division of its filaments of communication with the iris.

## Accommodation of the Eye for Vision at Different Distances.

Supposing the eye to be adapted to vision at an infinite distance, in which the rays from an object, as they strike the cornea, are practically parallel, it is evident that the foci of the rays, as they form a distinct image upon the retina, are all situated at the proper plane. Under these conditions, in a perfectly normal eye, the image, appreciated by the individual or seen by means of the ophthalmoscope, is perfectly clear and distinct. If the foci be situated in front of the retina, the rays, instead of coming to a focus upon a point in the retina, will cross, and from their diffusion or dispersion, will produce indistinct vision. Under these conditions a distinct point is not perceived, but every point in the image is surrounded by an indistinct circle. These are called "circles of diffusion." If, now, the eye, adjusted for vision at an infinite distance, be brought to bear upon a near object, the rays from which are divergent as they strike the cornea, the image will be no longer distinct, but will be obscured by circles of diffusion. It is the adjustment by which these circles of diffusion are removed, that constitutes accommodation. This fact has been demonstrated by Helmholtz by means of the ophthalmoscope. "If the eye be adjusted to the observation of an object placed at a certain distance, it is found that the image of a flame, placed at the same distance, is produced with perfect distinctness upon the retina, and, at the same time, upon the illuminated plane of the image, the vessels and the other anatomical details of the retina are seen with equal distinctness. But, when the flame is brought considerably nearer, its image becomes confused, while the details of the structure of the retina remain perfectly distinct."

It is evident that there is a certain condition of the eyes adapted to vision at an infinite distance, and that for the distinct perception of near objects, the transparent media must be so altered in their arrangement or in the curvatures of their surfaces, that the refraction will be greater; for without this, the rays would be brought to a focus beyond the retina.

The changes in the eye by which accommodation is effected are now known to consist mainly in an increased convexity of the lens for near objects; and the only points in dispute are a few unimportant details in the mechanism of this action. The simple facts to be borne in mind in studying this question are the following:

When the eye is accommodated to vision at an infinite distance, the parts are passive.

In the adjustment of the eye for near objects, the convexities of the lens are increased by muscular action.

In accommodation for near objects, the pupil is contracted; but this action is merely accessory and is not essential.

The ordinary range of accommodation varies between a distance of about five inches (12·7 centimetres) and infinity.

*Changes in the Crystalline Lens in Accommodation.*—It is important to determine the extent and nature of the changes of the lens in accommodation; and these changes have been accurately measured in the living subject. As the general results of these measurements (Helmholtz), it was ascertained that the lens becomes increased in thickness in accommodation for near objects, chiefly by an increase in its anterior curvature, by which this surface of the lens is made to project toward the cornea. As the iris is in contact with the anterior surface of the lens, this membrane is made to project in the act of accommodation. The posterior curvature of the lens is also increased, but this is slight as compared with the increase of the curvature of its anterior surface. The distance between the posterior surface of the lens and the cornea is not sensibly altered. It is unnecessary to describe minutely the methods employed in making these calculations, and it is sufficient to state that it is done by accurately measuring the comparative size of images formed by reflection from the anterior surface of the lens. The results obtained by Helmholtz, in observations upon two persons, are as follows:

| Persons examined. | Radius of curvature of the anterior surface of the lens. | | Displacement of the pupil in accommodation for near objects. |
|---|---|---|---|
| | Distant vision. | Near vision. | |
| O. H. | 0·4641 in. (11·9 mm.) | 0·3354 in. (8·6 mm.) | 0·0140 in. (0·36 mm.) |
| B. P. | 0·3432 in. (8·8 mm.) | 0·2701 in. (5·9 mm.) | 0·0172 in. (0·44 mm.) |

The mechanism of the changes in the thickness and in the curvatures of the lens in accommodation can be understood only by keeping clearly in mind the physical properties of the lens itself and its anatomical relations. *In situ*, in what has been called the indolent state of the eye, the lens is adjusted to vision at an infinite distance and is flattened by the tension of its suspensory ligament. After death, indeed, it is easy to produce changes in its form by applying traction to the zone of Zinn. Remembering the exact relations of the suspensory ligament, the ciliary muscle and the lens, and keeping in mind the tension within the globe, it is evident that when the ciliary muscle is in repose, the capsule will compress the lens, increasing its diameter and diminishing its convexity. It is in this condition that the eye is adapted to vision at an infinite distance. It is evident, also, that very slight changes in the convexity of the lens will be sufficient for the range of accommodation required. If any near object be fixed with the eye there is a conscious effort, and the prolonged vision of near objects produces a sense of fatigue. This may be illustrated by the very familiar experiment of looking at a distant object through a gauze. When the object is seen distinctly, the gauze is scarcely perceived; but by an effort the eye can be brought to see the meshes of the gauze distinctly, when the impression of the distant object is either lost or becomes very indistinct.

The ciliary muscle arises from the circular line of junction of the cornea and sclerotic, passes backward, and is lost in the tissue of the choroid, extending as far as the anterior border of the retina. Most of the fibres pass directly backward, but some become circular or spiral. When this muscle contracts, the choroid is drawn forward, with probably a slightly spiral motion of the lens, the contents of the globe, situated behind the lens, are compressed, and the suspensory ligament is relaxed. The lens itself, the compressing and flattening action of the suspensory ligament being dimin-


FIG. 256.—*Section of the lens etc., showing the mechanism of accommodation* (Fick).
The left side of the figure (*F*) shows the lens adapted to vision at infinite distances. The right side of the figure (*N*) shows the lens adapted to the vision of near objects, the ciliary muscle being contracted and the suspensory ligament of the lens consequently relaxed.

ished, becomes thicker and more convex, by virtue of its own elasticity, in the same way that it becomes thicker after death, when the tension of the ligament is artificially diminished.

This is in brief the mechanism of accommodation. Near objects are seen distinctly by a voluntary contraction of the ciliary muscle, the action of which is perfectly adapted to the requirements of vision. In early life the lens is soft and elastic, and the accommodating power is at its maximum; but in old age the lens becomes flattened, harder and less elastic, and the power of accommodation necessarily is diminished.

*Changes in the Iris in Accommodation.*—The size of the pupil is sensibly diminished in accommodation of the eye for near objects. Although the movements of the iris are directly associated with the muscular effort by which the form of the lens is modified, the contraction of the pupil is not one of the essential conditions of accommodation. Helmholtz reported a case in which the iris was completely paralyzed, the power of accommodation remaining perfect; and he described another case, reported by Von Graefe, in which accommodation was not disturbed after loss of the entire iris.

It has already been noted that the pupil contracts when the eyes are made to converge by the action of the muscles animated by the third pair of nerves; and it is evident that convergence of the eyes occurs in looking at very near objects. It has been shown by Donders, that increased convergence of the visual lines without change of accommodation makes the pupil contract, as is easily proved by simple experiments with prismatic glasses, and that when accommodation is effected without converging the visual axes, "each stronger tension is combined with contraction of the pupil." Contraction of the pupil, therefore, occurs both in convergence of the visual axes without accommodation and in accommodation for near objects without convergence of the eyes.

The action of the iris, as is evident from the facts just stated, is to a certain extent under the control of the will; but it can not be disassociated, first, from the voluntary action of the muscles which converge the visual axes, and second, from the action of the ciliary muscle. Donders, by alternating the accommodation for a remote and a near object, was able to voluntarily contract and dilate the pupil more than thirty times in a minute. Brown-Séquard, in discussing the voluntary movements of the iris, has mentioned a case in which "the pupil could be contracted or dilated without changing the position of the eye or making an effort of adaptation for a long or a short distance." As a farther evidence of the connection of accommodation with muscular action, cases are cited in works on ophthalmology, in which there is paralysis of the ciliary muscle, as well as cases in which the act of accommodation is painful.

A curious phenomenon connected with accommodation may be observed in looking at a near object through a very small orifice, like a pinhole. The shortest distance at which one can see a small object distinctly is about five inches (12·7 centimetres); but in looking at the same object through a pinhole in a card, it can be seen distinctly at the distance of about one inch (25·4 mm.), and it then appears considerably magnified. In this experiment, the card serves as a diaphragm with a very small opening, so that the centre of the lens only is used; and the apparent increase in the size of the object probably is due to the fact that its distance from the eye is many times less than the distance at which distinct vision is possible under ordinary conditions. It is well known that myopic persons, by being able to bring the eye nearer to objects than is possible in ordinary vision, can see minute details with peculiar distinctness.

*Erect Impressions produced by Images inverted upon the Retina.*—The images which make visual impressions are necessarily inverted upon the retina; but the cerebral visual centre takes no cognizance of this, and objects are seen in their actual position. It seems almost absurd to enter into a serious discussion of this fact. In the words of Helmholtz, "our natural consciousness is completely ignorant even of the existence of the retina and of the formation of images: how should it know any thing of the position of images formed upon it?"

*Field of Indirect Vision.*—If the eye be kept fixed upon a certain point, and an object be moved from this point as a centre in lines radiating in different directions until it passes from the field of view, the limits of indirect vision are indicated. Eight or ten such points of limit, connected by a curved line, give a map of the visual field. This may be done roughly upon a flat surface, such as a blackboard, placed at a distance of twelve to eighteen inches (3 to 4·5 centimetres) from the eye, or a chart may be made with an instrument called the perimeter, by which the field is marked on the inner surface of a hemisphere. The field of vision thus delineated is an irregular oval, extending from the fixed point, farther to the temporal side than to either the nasal side or above and below. The extent from the fixed point is about 90° on the temporal side, and about 70° to the nasal side and above and below. The field for white is larger than for colors, especially on its nasal side, as is seen in Fig. 257. The field is smallest for green, a little larger for red, and is larger still for blue. Investigation of the field of indirect vision with the perimeter is very useful in ophthalmology, but the chief physiological interest, as regards the sensibility of the retina, is connected with direct vision.

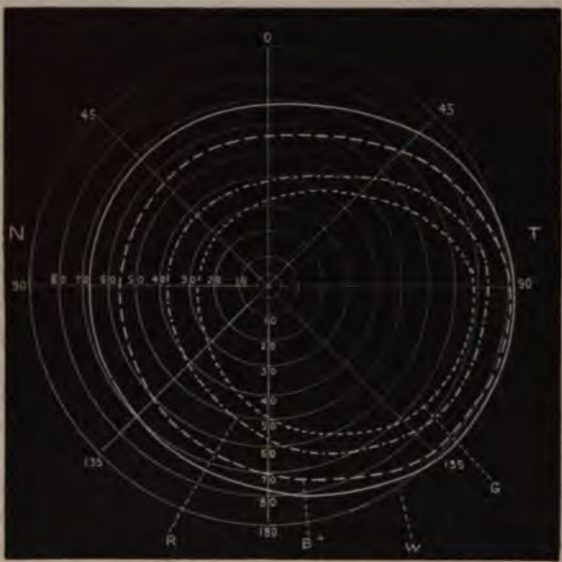


FIG. 257.—*Field of vision of the right eye, as projected by the patient on the inner surface of a hemisphere, the pole of which forms the object of regard.*—Semi-diagrammatic (Nettleship, after Landolt).
T, temporal side; N, nasal side; W, boundary for white; B, boundary for blue; R, boundary for red; G, boundary for green.

## BINOCULAR VISION.

Thus far the mechanism of the eye and its action as an optical instrument, in monocular vision only, have been described; but it is evident that both eyes are habitually used, and that their axes are practically parallel in looking at distant objects and are converged when objects are approached to the nearest point at which there is distinct vision. In fact an image is formed simultaneously upon the retina of each eye, but it is nevertheless appreciated as a unit. If the axis of one eye be slightly deviated by pressure upon the globe, so that the images are not formed upon corresponding points in the retina of each eye, vision is more or less indistinct and is double. In strabismus, when this condition is recent, temporary or periodical, as in recent cases of paralysis of the external rectus muscle, when both eyes are normal, there is double vision. When the strabismus is permanent and has existed for a long time, double vision may not be observed, unless the subject direct the attention strongly to this point. As but one eye is capable of fixing objects accurately, images are formed upon the fovea of this eye only. Images formed upon the retina of the other eye are indistinct, and in many instances are habitually disregarded; so that practically the subject uses but one eye, and presents the errors of appreciation which attend monocular vision, such as a want of exact estimation of the solidity and distance of objects. It is stated as the rule that when strabismus of long standing is remedied, as far as the axes of the eyes are concerned, by an operation, binocular vision is not restored. This is explained upon the supposition that the perceptive power of the retina of the affected eye has been gradually and irrecoverably lost from disuse. In normal binocular vision the images are formed upon the fovea centralis of each eye; that is, upon corresponding points, which are, for each eye, the centres of distinct vision. The concurrence of both eyes is necessary to the exact appreciation of distance and form; and when the two images are formed upon corresponding points, the visual centre receives a correct impression of a single object. When vision is perfect, the sensation of the situation of any single object is referred to one and the same point; and the impression of a double image can not be received unless the conditions of vision be abnormal.

*Corresponding Points.*—While it is evident, after the statements just made, that an image must be formed upon the fovea of each eye in order to produce the effect of a single object, it becomes important to ascertain how far it is necessary that the correspondence of points be carried out in the retina. It is almost certain that for absolutely perfect, single vision with the two eyes, the impressions must be made upon exactly corresponding points, even to the ultimate, sensitive elements of the retina. It may be assumed, indeed, that each rod and each cone of one eye has its corresponding rod and cone in the other, situated at exactly the same distance and in corresponding directions from the visual axis. When the two images of an object are formed upon these corresponding points, they appear as one; but when the images do not correspond, the impression is as though the images were formed upon different points in one retina, and of necessity they appear double.

The effect of a slight deviation from the corresponding points may be illustrated by the following experiment: If a small object, like a lead-pencil, held at a distance of a few inches, be fixed with the eyes, it is seen distinctly as a single object. Holding another small object in the same line, a few inches farther removed, when the first is seen distinctly, the second appears double. If the second object be fixed with the eyes, the first appears double. It is evident here, that when the axes of the eyes bear upon one of these objects, the images of the other must be formed at a certain distance from the corresponding retinal points.

*The Horopter.*—The above-mentioned experiment affords an explanation of the horopter. If both eyes be fixed upon a point directly in front and be kept in this position, an object moved to one side or the other, within a certain area, may be seen without any change in the direction of the axis of vision; but the distance from the eye at which there is single vision of this object is fixed, and at any other distance the object appears double. The explanation of this is that at a certain distance from the eye, the images are formed upon corresponding points in the retina; but at a shorter or longer distance, this can not occur. This illustrates the fact that there are corresponding points in a large part of the sensitive layer of the retina, as well as in the fovea centralis. By these experiments, the following facts have been ascertained: With both eyes fixed upon an object, another object moved to one side or the other can be distinctly seen only when it is carried in a certain curved line. On either side of this line, the object appears double. This line, or area—for the line may have any direction—is called the horopter. It was supposed at one time to be a regular curve, or a portion of a circle drawn through the fixed point and the points of intersection of the rays of light in each eye. Although it has been ascertained that the line varies somewhat from a regular curve, and also varies in different meridians, this is due to differences in refraction, etc., and the principle is not altered.

If the visual areas of the two retinæ be superimposed, the fixation-points coinciding, it becomes evident that a portion only of the two fields can have corresponding points. This is the light portion shown in Fig. 258, which may be called the binocular field of vision. Binocular vision must be impossible in the temporal portion of each visual area (Nettleship).

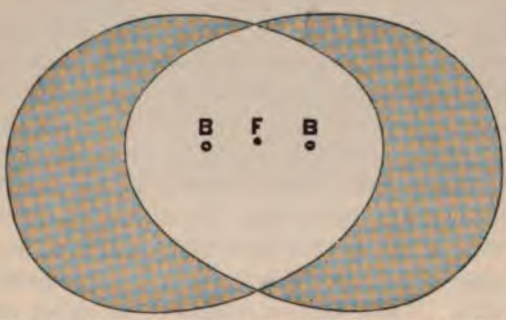

FIG. 258.—*Binocular field of vision* (Nettleship, after Förster.) F, fixation-point; B, B, blind spots.

It is undoubtedly true that education and habit have a great deal to do with the correction of visual impressions and the just appreciation of the size, form and distance of objects. In the remarkable case of Casper Hauser, who is said to have been kept in total darkness and seclusion, from the age of five months until he was nearly seventeen years old, the appreciation of size, form and distance were acquired by correcting and supplementing the sense of sight, by experience. This boy at first had no idea of the form of objects or of distance, until he had learned by touch, by walking etc., that certain objects were round and others were square, and had actually traversed the distance from one object to another. At first all objects appeared as if painted upon a screen. Such points as these it would be impossible to accurately observe in infants; but young children often grasp at remote objects, apparently under the impression that they were within reach. It must be admitted, however, that the account of the case of Casper Hauser is rather indefinite; but it is certain that even in the adult, education and habit greatly improve the faculty of estimating distances.

Careful observations leave no doubt of the fact that monocular vision is incomplete and inaccurate, and that it is only when two images are formed, one upon either retina, that vision is absolutely perfect. The sum of actual knowledge upon this important point is expressed in the following quotation from Giraud-Teulon:

" Monocular vision only indicates to us immediately, visual direction, and not precise locality. At whatever distance a luminous point may be situated in the line of direction, it forms its image upon the same point in the retina.

" In the physiological action of a single eye, in order to arrive at an idea of the distance of a point in a definite direction, we have only the following elements:

" 1. The consciousness of an effort of accommodation.

" 2. Our own movement in its relations to the point observed.

" 3. Facts brought to bear from recollection, education, our acquired knowledge with regard to the form and size of objects: in a word, experience.

" 4. The geometric perspective of form and position.

" 5. Aërial perspective.

" All these are elements wanting in precision and leaving the problem without a decisive solution.

" And, indeed:

" We place before one of our eyes, the other being closed, the excavated mould of a medallion: we do not hesitate, after a few seconds, to mistake it for the relief of the medallion. This illusion ceases at the instant that both eyes are opened.

" Or again:

" A miniature, a photograph, a picture, produces for a single eye a perfect illusion; but if both eyes be open, the picture becomes flat, the prominences and the depressions are effaced.

" We may repeat the following experiment described by Malebranche: 'Suspend by a thread a ring, the opening of which is not directed toward us; step back two or three paces; take in the hand a stick curved at the end; then, closing one eye with the hand, endeavor to insert the curved end of the stick within the ring, and we shall be surprised at being unable to do in a hundred trials what we should believe to be very easy. If, indeed, we abandon the stick and endeavor to pass one of the fingers through the ring. we shall experience a certain degree of difficulty, although it is very near. This difficulty ceases at the instant that both eyes are opened.'

" As regards precision, exactitude of information concerning the relative distance of objects, that is to say, the idea of the third dimension, or of depth, there is then a notable difference between binocular vision and that which is obtained by means of one eye alone."

It is evident that an accurate idea of the distance of near objects can not be obtained except by the use of both eyes, and this fact will partly explain the errors of monocular vision in looking with one eye upon objects in relief; for under these conditions, it is impossible to determine with accuracy whether the points in relief be nearer or farther from the eye than the plane surface. This will not fully explain, however, the idea of solidity of objects, which is obtained by the use of both eyes; for the estimation of distance is obtained by bringing the axes of both eyes to bear upon a single object, be it near or remote. The fact is—as was distinctly stated by Galen, in the second century—that in looking at any solid object not so far removed as to render the visual axes practically parallel, a portion of the surface, seen with the right eye, is not seen with the left eye, and *vice versâ*. The two impressions, therefore, are not identical for each retina; the image upon the left retina including a portion of the left side of the object, not seen by the right eye, the right image in the same way including a portion of the right surface, not seen by the left eye. These slightly dissimilar impressions are fused and produce the impression of a single image, when vision is perfectly normal; and this gives the idea of relief or solidity, and an exact appreciation of the form of objects, when they are not too remote.

The fact just stated is of course a mathematical necessity in binocular vision for near objects; but the actual demonstration of the fusion of two dissimilar images and the consequent formation of a single image giving the impression of solidity was made by the invention of the stereoscope, by Wheatstone. The principle of this instrument is very simple. Two pictures are made, representing a solid object, one viewed slightly from the right side, and the other, slightly from the left, so as to imitate the differences in the images formed upon the two retinæ. These pictures are so placed in a box that the image of one is formed upon the right retina, and the other, upon the left. When these conditions are accurately fulfilled, but a single image is seen, and this conveys to the mind the perfect illusion of a solid object. Experiments with the stereoscope are so familiar that they need hardly be dwelt upon. Experience, the aid of the sense of touch etc., enable persons with but one eye to get a notion of form, but the impressions are never entirely accurate in this regard, although, from habit, this defect occasions little or no inconvenience.

Although an opposite opinion is held by some experimenters, Helmholtz, with many others, has stated that when one color is seen with one eye and another color, with the other eye, in the stereoscope, the impression is not of a single color resulting from the combination of the two. It is true that there is an imperfect mingling of the two colors, but this is very different from the resulting color produced by the actual fusion of the two. There is, in other words, a sort of confusion of colors, without the complete combination observed in ordinary experiments. One additional point of importance, however, is that the binocular fusion of two pictures, unequally illuminated or of different colors, produces a single image of a peculiar lustre, even when both surfaces are dull. This may be shown by making a stereoscopic combination of images of crystals, one with black lines on a white ground, and the other with white lines on a black ground. The resulting image has then the appearance of dark, brilliant crystals, like graphite.

*Duration of Luminous Impressions* (*After-Images*).—The time required for a single visual stimulation of the retina is exceedingly short. The letters on a printed page are distinctly seen when illuminated by an electric spark, the duration of which is not more than forty billionths of a second (Rood). An impression made upon the retina, however, endures for a length of time that bears a certain relation to the intensity of the luminous excitation. If the eyes be closed after looking steadily at a very bright object, the object is more or less distinctly seen after the rays have ceased to pass to the eye, and the image fades away gradually. When there is a rapid succession of images, they may be fused into one, as the spokes of a rapidly revolving wheel are indistinct and produce a single impression. This is due to the persistence of the successive retinal impressions; for if a revolving wheel or even a falling body be illuminated for the brief duration of an electric spark, it appears absolutely stationary, as the period of time necessary for perfectly distinct vision and the duration of the illumination are so short, that there is no time for any appreciable movement of the object. The familiar experiments made with revolving disks illustrate these points. In a disk marked with alternate, radiating lines of black and white, the rays become entirely indistinguishable during rapid revolution, and the disk appears of a uniform color, such as would be produced by a combination of the black and white. The effects of an artificial combination of colors may be produced in this way, the resultant color appearing precisely as if the individual colors had been ground together. The duration of retinal impressions varies considerably for the different colors. According to Emsmann, the duration for yellow is 0·25 of a second; for white, 0·25 of a second; for red, 0·22 of a second; and for blue, 0·21 of a second.

The impressions which remain on the retina after an object has been looked at steadily are called after-images. When these are bright and of the same character as the object, they are called positive after-images. When the stimulation of the retina has been very powerful and prolonged, the after-image frequently is dark. Such images are called negative after-images.

It is unnecessary to describe farther in detail the well known phenomena which illustrate the point under consideration. The circle of light produced by rapidly revolving a burning coal, the track of a meteor, and other illustrations, are sufficiently familiar, as well as many scientific toys producing optical illusions of various kinds.

*Irradiation.*—It has been observed that luminous impressions are not always confined to the elements of the retina directly involved, but are sometimes propagated to those immediately adjacent. This gives to objects a certain degree of amplification, which is generally in proportion to their brightness. An illustration of this is afforded by the simple experiment of looking at two circles, one black on a white ground, and the other white on a black ground. Although the actual dimensions of the two circles are identical, the irradiation of rays from the white circle makes this appear the larger. In a circle with one half black and the other white, the white portion will appear larger, for the same reason. These phenomena are due to what has been called irradiation; and their explanation is very simple. It is probable that luminous impressions are never confined absolutely to those parts of the retina upon which the rays of light directly impinge, but that the sensitive elements immediately contiguous are always more or less involved. In looking at powerfully illuminated objects, the irradiation is considerable, as compared with objects which send fewer luminous rays to the eye.

In experiments analogous to those just described, made with strongly colored objects, it has been observed that the border of irradiation takes a color complementary to that of the object itself. This is particularly well marked when the objects are steadily looked at for some time. Illustrations of this point also are very simple. In looking steadily at a red spot or figure on a white ground, a faint areola of a pale-green soon appears surrounding the red object; or if the image be yellow, the areola will appear pale-blue. These appearances have been called accidental areolæ.

### Movements of the Eyeball.

The eyeball nearly fills the cavity of the orbit, resting, by its posterior portion, upon a bed of adipose tissue, which is never absent, even in extreme emaciation. Outside of the sclerotic, is a fibrous membrane, the tunica vaginalis oculi, or capsule of Tenon, which is useful in maintaining the equilibrium of the globe. This fibrous membrane surrounds the posterior two-thirds of the globe and is loosely attached to the sclerotic. It is perforated by the optic nerve posteriorly, and by the tendons of the recti and oblique muscles of the eyeball in front, being reflected over these muscles. It is also continuous with the palpebral ligaments and is attached by two tendinous bands, to the border of the orbit, at the internal and the external angles of the lids.

The muscles which move the globe are six in number for each eye. These are the external and internal recti, the superior and inferior recti and the

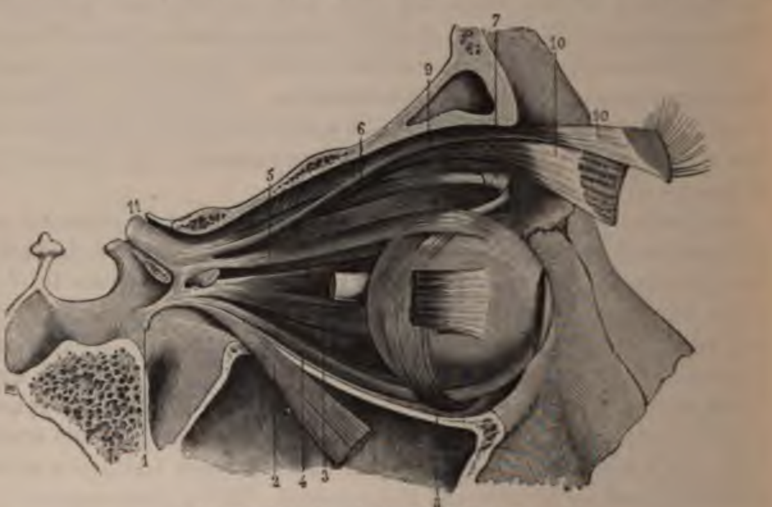


Fig. 259.—*Muscles of the eyeball* (Sappey).

1, attachment of the tendon connected with the inferior rectus, internal rectus and external rectus; 2, external rectus, divided and turned downward, to expose the inferior rectus; 3, internal rectus; 4, inferior rectus; 5, superior rectus; 6, superior oblique; 7, pulley and reflected portion of the superior oblique; 8, inferior oblique; 9, levator palpebri superioris; 10, 10, middle portion of the levator palpebri superioris; 11, optic nerve.

two oblique muscles. The four recti muscles and the superior oblique arise posteriorly from the apex of the orbit. The recti pass directly forward by the sides of the globe and are inserted by short, tendinous bands into the sclerotic, at a distance of one-fourth to one-third of an inch (6·4 to 8·5 mm.) from the margin of the cornea. The superior oblique, or trochlearis muscle passes along the upper and inner wall of the orbit, to a point near the inner angle. It here presents a rounded tendon, which passes through a ring, or pulley of fibro-cartilage; and it is from this point that its action is exerted upon the globe. From the pulley, or trochlea, the tendon becomes flattened, passes outward and backward beneath the superior rectus, and is inserted into the sclerotic, about midway between the superior and the external rectus and just behind the equator of the globe. The inferior oblique muscle arises just within the anterior margin of the orbit, near the inner angle of the eye, and passes around the anterior portion of the globe, beneath the inferior rectus and between the external rectus and the eyeball, taking a direction outward and slightly backward. Its tendon is inserted into the sclerotic, a little below the insertion of the superior oblique. The general arrangement of these muscles is shown in Fig. 259.

The various movements of the eyeball are easily understood by a study of the associated movements of the muscles just enumerated, at least as far as is necessary to the comprehension of the mechanism by which the eyes are directed toward any particular object. The centre of exact vision is in the fovea; and it is evident that in order to see any object distinctly, it is necessary to bring it within the axes of vision of both eyes. As the globe is so balanced in the orbit as to be capable of rotation, within certain limits, in every direction, it is necessary only to note the exact mode of action of each of the muscles, in order to comprehend how the different movements are accomplished; and it is sufficient for practical purposes to admit that approximately there is a common axis of rotation for each pair of muscles.

Under ordinary conditions, in the human subject, the action of the six ocular muscles is confined to the movements of rotation and torsion of the globe. It is said that in the human subject, there is no such thing as protrusion of the eye from general relaxation of these muscles, and that it is impossible, by a combined action of the four recti muscles, to retract the globe in the orbit; but those who have operated upon the eyes assert positively that this statement is erroneous, and that the globe is almost always suddenly and powerfully drawn within the orbit, when a painful impression is made upon the cornea. This is stated as a matter of common observation by ophthalmic surgeons.

The extent to which the line of vision may be turned by a voluntary effort varies in different individuals, even when the eyes are perfectly normal. In myopic eyes, the centre of rotation is deeper in the orbit than normal, and the extent of the possible deviation of the visual line is correspondingly diminished. Helmholtz stated that, in his own person, with the greatest effort that he was capable of making, he could move the line of vision in the horizontal plane to the extent of about fifty degrees, and in the vertical plane, about forty-five degrees; but he added that these extreme rotations were very forced, and that they could not be sustained for any considerable length of time. It is probable that the eyeball is seldom moved to an angle of forty-five degrees, the direction of the visual line being more easily accomplished by movements of the head.

*Action of the Recti Muscles.*—The internal and external recti rotate the globe upon a vertical axis, which is perpendicular to the axis of the eye. The isolated action of these muscles, particularly of the external rectus, is often illustrated in certain forms of paralysis, which have been alluded to in connection with the history of the cranial nerves.

The superior and inferior recti rotate the globe upon an horizontal axis, which is not at right angles with the axis of the eye, but is inclined from the nasal side, slightly backward. The line which serves as the axis of rotation for these muscles forms an angle of about seventy degrees with the axis of the globe; and as a consequence of this arrangement, their action is not so simple as that of the internal and external recti. The insertion of the superior rectus in such, that when it contracts, the pupil is directed upward and inward, the inferior rectus directing the pupil downward and inward.

The above represents the simple, isolated action of each pair of recti muscles; but it is easy to see how, without necessarily involving the action of the oblique muscles, the globe may be made to perform a great variety of rotations, and the line of vision may be turned in nearly every direction, by the action of the recti muscles alone.


FIG. 260.—*Diagram illustrating the action of the muscles of the eyeball* (Fick).

The heavy lines represent the muscles of the eyeball, and the fine lines, the axes of the superior and the inferior recti and the axes of the oblique muscles.

*Action of the Oblique Muscles.*—It is sufficient for all practical purposes to assume that the superior and the inferior oblique muscles act as direct antagonists to each other. The most exact measurements show that the axis of rotation for these muscles is horizontal and has an oblique direction from before backward and from without inward. The angle formed by the axis of rotation of the oblique muscles with the axis of the globe is thirty-five degrees; and the angle between the axis of the oblique muscles and the axis of the superior and inferior recti muscles is seventy-five degrees.

Given the direction of the axis of rotation and the direction of the superior oblique muscle, it is easy to understand the effects of its contraction. As this muscle, passing obliquely backward and forward over the globe, acts from the pulley near the inner angle of the eye, to its insertion just behind the anterior half of the globe on its external and superior surface (7, Fig. 259), it must rotate the globe so as to direct the pupil downward and outward.

The inferior oblique, passing outward and slightly backward under the globe, acts from its origin, at the margin of the orbit near the inner angle of the eye, to its insertion, which is just below the insertion of the superior oblique. This muscle rotates the globe so as to direct the pupil upward and outward.

The action of the oblique muscles seems to be specially connected with the movements of torsion of the globe. It is necessary to distinct, single vision with both eyes, that the images should be formed upon exactly corresponding points on the retina, and that they should bear, for the two eyes, corresponding relations to the perpendicular. Thus it is that when the head is inclined to one side, the eyes are twisted upon an oblique, antero-posterior axis; as can be readily seen by observing little spots upon the iris, during these movements.

The superior oblique muscle is supplied by a single nerve, the patheticus. When this muscle is paralyzed, the inferior oblique acts without its antagonist, and the eyeball is immovable, as far as the twisting of the globe, just described, is concerned. When the head is moved toward the shoulder, the globe can not rotate to maintain a position corresponding to that of the other eye, and there is double vision. This point has already been touched upon in connection with the physiology of the nerves of the eyeball and the situation of corresponding points in the retina.

*Associated Action of the Different Muscles of the Eyeball.*—It is almost unnecessary to add, after the description just given of the actions of the individual muscles of the globe, that their contractions may be associated so as to produce a great variety of movements. There is no consciousness, under ordinary conditions, of the muscular action by which the globe is rotated and twisted in various directions, except that by an effort of the will the line of vision is directed toward different objects. By a strong effort the axis of the eyes may be converged by contracting both internal recti, and some persons can produce extreme divergence by using both external recti; but this is abnormal.

In looking at distant objects the axes of vision are practically parallel. In looking at near objects the effort of accommodation is attended with the degree of convergence necessary to bring the visual axes to bear upon identical points. In looking around at different objects the head is moved more or less and the globes are rotated in various directions. In the movements of the globes vertically the axes are kept parallel, or at the proper angle, by the internal and external recti, and the superior and inferior recti upon the two sides act together. In rotating the globe from one side to the other, upon a vertical axis, the external rectus upon one side acts with the internal rectus upon the other. In the movements of torsion upon an antero-posterior axis there must be an associated action of the oblique muscles and the recti.

An important point, not to be lost sight of in the study of the associated action of the muscles of the globe, relates to the associated movements of the two eyes. Perfect, binocular vision is possible only when impressions are made upon exactly corresponding points in the retina of each eye. If one eye be deviated in the horizontal plane, the points no longer correspond, and there is double vision, the same as if two impressions were made upon one retina; for when the impressions exactly correspond, the two retinæ act practically as a single organ. The same is true in deviation of the globe in the vertical plane. If it be supposed, for the sake of argument, that the retina is square, it is evident that a torsion, or twisting of one globe upon an antero-posterior axis, must be attended with an analogous movement of the other globe, in order to bring the visual rays to bear upon the corresponding points; in other words, the obliquity of the assumed square of the retina must be exactly the same for the two eyes, or the coincidence of the corresponding points would be disturbed and there would be double vision. Deviation of one eye in the horizontal or the vertical plane disturbs the relation of the corresponding points, and a deviation from exact coincidence of action in torsion of the globes, twists, as it were, the corresponding points, so that their relation is also disturbed. It is evident, therefore, that the varied movements of the globes, by the combined action of the recti and oblique muscles, must correspond for each eye, in the movements of torsion upon an antero-posterior axis as well as in movements of rotation upon the horizontal or the vertical axis.

### Centres for Vision.

Experiments have been made upon the lower animals by Ferrier, Munk, Exner, Dalton and many others, with the object of locating in the cerebrum a centre for vision. It is important, however, to compare the results of such experiments with cases of cerebral lesions in the human subject. As the general result of experiments, both on dogs and monkeys, and of pathological observations, the present opinion is that the centres for vision are in the occipital lobes. The lower half of the cuneus and the adjacent portions of the middle occipital convolutions (compare Figs. 221 and 222) seem to be the cerebral terminations of fibres that are continuous with the optic tracts. These fibres are not crossed in the cerebrum, but the conductors decussate at the optic chiasm, as they pass to the eyes. Cases have been observed in the human subject, in which lesion of these parts on one side has been followed by loss of vision in one lateral half of the retina in either eye. This condition is called hemianopsia. In these instances the blindness is confined to the temporal side of the retina corresponding to the lesion and the nasal side of the retina of the opposite eye. This is called lateral, homonymous hemianopsia, and this is the form which always occurs in unilateral, cerebral lesion. In dogs and in monkeys destruction of both occipital lobes and both angular convolutions produces total and permanent blindness of both eyes.

The complete and perfect perception of visual impressions involves intellectual action connected with the simple visual sense. An individual may see objects and yet not be able to appreciate their significance. In the condition known as word-blindness, words are seen, but they convey no idea. A dog with part of the occipital lobes removed may see objects, such as food, but does not recognize their character. There are, apparently, psychical centres, which elaborate the impressions received by the visual centres.

What seems at present to be the most rational view to take with regard to the location and action of the visual centres is the following, which has been adopted and formulated by Hun:

1. In the lower half of the cuneus and the adjacent part of the median occipito-temporal convolution, is the centre for simple, visual sensation. This part is connected with fibres from homonymous halves of the retina of each eye, the temporal half of the retina of the same side and the nasal half of the retina of the opposite side.

2. The action of the cortex of the convex surface of the temporal lobe (perhaps only on the left side) "is necessary for full visual perception and recognition, and for the production of visual memories." This may be called the psychical, visual centre. Psychical blindness may exist, indeed, without loss of visual sensation.

3. The angular convolution is not a visual centre, as was claimed by Ferrier. It is related to visual perception only in so far as it affects "the memories of the appearance of written or printed words." In cases of word-blindness lesions have been found in this situation (Stirling).

The situation of the visual centres, as indicated above, is in parts supplied by the third branch of the posterior cerebral artery.

*Perception of Colors.*—Physical researches have shown that different colors have different wave-lengths. It is evident that they are appreciated by the visual centres, as distinct impressions for each color and shade of color, although, under what may be called normal conditions, the delicacy of color-perception varies in different individuals. Color-blindness is an abnormal condition, in which the power of discrimination between different colors is impaired or lost. Some persons are entirely insensible to colors; and cases have been reported in which one eye was color-blind, while the other eye was normal (Becker and Hippel). The latter is called unilateral color-blindness.

Before the cerebral visual centres had been described, various theories were proposed to account for the perception of colors. Some physiologists assumed the existence of separate and distinct elements in the retina for the reception of impressions made by different colors; but this and other theories have been far from satisfactory. Cases of disease of the brain, in which ordinary visual sensations remain but the sense of color is destroyed, seem to show that a part of the visual centre is specially connected with the appreciation of colors. Beyond this, nothing is known of the mechanism of color-perception.

## Parts for the Protection of the Eyeball.

The orbit, formed by the union of certain of the bones of the face, receives the eyeball, the ocular muscles, the muscle of the upper lid, blood-vessels, nerves and a part of the lachrymal apparatus; and it contains, also, a certain quantity of adipose tissue, which latter never disappears, even in extreme marasmus. The bony walls of this cavity protect the globe and lodge the parts above enumerated. The internal, or nasal wall of the orbit projects considerably beyond the external wall, so that the extent of vision is far greater in the outward than in the inward direction. As the globe is more exposed to accidental injury from an outward direction, the external wall of the orbit is strong, while the bones which form its internal wall are comparatively fragile. The upper border of the orbit (the superciliary ridge) is provided with short, stiff hairs (the eyebrows) which serve to shade the eye from excessive light and to protect the eyelids from perspiration from the forehead.

The eyelids are covered by a very thin integument and are lined by the conjunctival mucous membrane. The subcutaneous connective tissue is thin and loose and is entirely free from fat. The skin presents a large number of short papillæ and small, sudoriparous glands. At the borders of the lids, are short, stiff, curved hairs, arranged in two or more rows, called the eyelashes or cilia. Those of the upper lid are in greater number and longer than the lower cilia. The curve of the lashes is from the eyeball. They serve to protect the globe from dust, and to a certain extent, to shade the eye.

The tarsal cartilages are small, elongated, semilunar plates, extending from the edges of the lids toward the margin of the orbit, between the skin and the mucous membrane. Their length is about an inch (25·4 mm.). The central portion of the upper cartilage is about one-third of an inch (8·5 mm.) broad, and the corresponding part of the lower cartilage measures about one-sixth of an inch (4·2 mm.). At the inner canthus, or angle of the eye, is a small, delicate ligament, or tendon, the tendo palpebrarum, which is attached to the lachrymal groove internally, passes outward, and divides into two lamellæ, which are attached to the two tarsal cartilages. At the outer canthus the cartilages are attached to the malar bone, by the external tarsal ligament. The tarsal cartilages receive additional support from the palpebral ligament, a fibrous membrane attached to the margin of the orbit and the convex border of the cartilages and lying beneath the orbicularis muscle. This membrane is strongest near the outer angle of the eye.

On the posterior surface of the tarsal cartilages, partly embedded in them and lying just beneath the conjunctiva, are the Meibomian glands. The structure and uses of these glands have already been described in connection with the physiology of secretion. They produce an oily fluid, which smears the edges of the eyelids and prevents the overflow of tears.

*Muscles which open and close the Eyelids.*—The corrugator supercilii draws the skin of the forehead downward and inward; the orbicularis palpebrarum closes the lids; and the levator palpebræ superioris raises the upper lid. The tensor tarsi, called the muscle of Horner, is a very thin, delicate muscle, which is regarded by some anatomists as a deep portion of the orbicularis. Considering this as a distinct muscle, it consists of two delicate slips, which pass from either eyelid, behind the lachrymal sac, uniting here to go to its attachment at the posterior portion of the lachrymal bone. When this acts with the orbicularis, it compresses the lachrymal sac.

The orbicularis palpebrarum is a broad, thin muscle, closely attached to the skin, surrounding the free margin of the lids, and extending a short distance over the bones, beyond the margin of the orbit. This muscle may be described as arising from the tendo palpebrarum, the surface of the nasal process of the superior maxillary bone and the internal angular process of the os frontis. From this origin at the inner angle of the eye, its fibres pass elliptically around the fissure of the lids, as above indicated. Its action is to close the lids. In the ordinary, moderate contraction of this muscle, only the upper lid is moved; but in forcible contraction, the lower lid moves slightly and the lids are drawn toward the nose.

The levator palpebræ superioris is situated within the orbit. It arises from a point a little above and in front of the optic foramen, at the apex of the orbit, passes forward above the eyeball, and spreads into a thin tendon, which is inserted into the anterior surface of the superior tarsal cartilage. Its action is to raise the upper lid. This muscle and its relations are shown in Fig. 259 (9, 10, 10), page 718.

In the act of opening the eyes the levator muscles alone are brought into play. Closing of the lids is accomplished by the orbicular muscles. Both of these sets of muscles act to a great extent without the intervention of the will. The eyes are kept open almost involuntarily, except in extreme fatigue; although when the will ceases to act the lids are closed. Nevertheless there is hardly a conscious effort usually in keeping the eyes open, and an effort is required to close the eyes. During sleep the eyes are closed and the globes are turned upward. The contractions of the orbicular muscles which take place in winking usually are involuntary. This act occurs at short intervals, and it is useful in spreading the lachrymal secretion over the exposed portions of the globes. The action of both sets of muscles usually is simultaneous, although they may be educated so as to close one eye while the other is kept open. The action of the orbicularis is so far removed from the control of the will, that when the surface of the globe is touched or irritated or when the impression of light produces intense pain, it is impossible to keep the eye open.

*Conjunctival Mucous Membrane.*—The entire inner surface of the upper and lower eyelids is lined by a mucous membrane, which is reflected forward, from the inner periphery of the lids, over the eyeball. The membrane lining the lids is called the palpebral conjunctiva, and that covering the eyeball, the ocular conjunctiva. The latter presents a sclerotic and a corneal portion. The conjunctiva presents a superior and an inferior fold, where it is reflected upon the globe. In the superior conjunctival fold, are glandular follicles, or accessory lachrymal glands, which secrete a certain portion of the fluid which moistens the surface of the eyeball. These are generally described as forming a part of the lachrymal gland. At the inner canthus there is a vertical fold, the plica semilunaris, with a reddish, spongy elevation at its inner portion, called the caruncula lacrymalis. The caruncula presents a collection of follicular glands, with a few delicate hairs on its surface. The conjunctiva is continuous with the membrane of the lachrymal ducts, of the puncta lachrymalia and of the Meibomian glands. Beneath the conjunctiva, except in the corneal portion, is a loose, connective tissue.

The palpebral conjunctiva is reddish, thicker than the ocular portion, furrowed, and presents small, isolated papillæ near the borders of the lids, which increase in number and size toward the folds. This portion of the membrane presents large, capillary blood-vessels and lymphatics and is covered with a layer of cells of flattened epithelium. The sclerotic portion is thinner, less vascular, and has no papillæ. It is covered by conical and rounded epithelial cells, in two to four layers. Over the cornea the epithelium of the sclerotic portion is continued in delicate, transparent layers, without a distinct basement-membrane.

*The Lachrymal Apparatus.*—The eyeball is constantly bathed in a thin, watery fluid, which is secreted by the lachrymal gland, is spread over the globe by the movements of the lids and of the eyeball, and is prevented, under ordinary conditions, from overflowing upon the cheek, by the Meibomian secretion. The excess of this fluid is collected into the lachrymal sac, and is carried into the nose, by the nasal duct. The lachrymal gland, the lachrymal canals, duct and sac, and the nasal duct constitute the lachrymal apparatus.

The lachrymal gland is an ovoid, flattened gland of the racemose variety, resembling the salivary glands in its general structure. It is about the size of a small almond and is lodged in a shallow depression in the bones of the orbit, at its upper and outer portion. It is closely attached to the periosteum, by its upper surface, and is moulded below to the convexity of the globe. Its anterior portion is separated from the rest by a well marked groove, is comparatively thin and adheres to the upper lid. It presents six to eight (usually seven) ducts, which form a row of openings into the conjunctival fold. Five or six of these orifices are situated above the outer canthus, and two or three open below. In its minute structure this gland presents no points of special physiological importance as distinguished from the ordinary racemose glands.

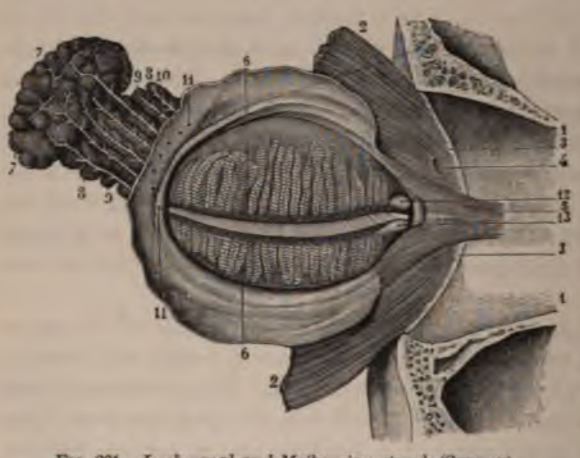

FIG. 261.—*Lachrymal and Meibomian glands* (Sappey).

1, 1, internal wall of the orbit; 2, 2, internal portion of the orbicularis palpebrarum; 3, 3, attachment of this muscle to the orbit; 4, orifice for the passage of the nasal artery; 5, muscle of Horner; 6, 6, posterior surface of the eyelids, with the Meibomian glands; 7, 7, 8, 8, 9, 9, 10, lachrymal gland and ducts; 11, openings of the lachrymal ducts.

It receives nervous filaments from the fifth cranial nerve and the sympathetic.

The channels by which the excess of tears is conducted into the nose begin by two little points, situated on the margin of the upper and the lower lid, near the inner canthus, called the puncta lacrymalia, which present each a minute orifice. These orifices open respectively into the upper and the lower lachrymal canals, which together surround the caruncula lacrymalis. At the inner angle, just beyond the caruncula, the two canals join, to empty into the lachrymal sac, which is the dilated upper extremity of the nasal duct. The duct is about half an inch (12·7 mm.) in length and empties into the inferior meatus of the nose, taking a direction nearly vertical and inclined slightly outward and backward. This portion of the lachrymal apparatus is fibrous and is lined by a reddish, mucous membrane, which presents several well marked folds. Near the puncta, are two folds, one for each lachrymal canal. Another pair of folds exists near the horizontal portions of the canals. At the opening of the duct into the nose, is an overhanging fold of the nasal, mucous membrane. These folds are supposed to prevent the reflux of fluid from the lachrymal canals and the entrance of air from the nose. The mucous membrane of the lachrymal canals is covered by a flattened epithelium, like that of the conjunctiva. The lachrymal sac and duct are lined by a continuation of the ciliated epithelium of the nose. The disposition of the apparatus just described is shown in Fig. 262.

*The Tears.*—The secretion of the lachrymal glands is constant, although the quantity of fluid may be increased under various conditions. The actual quantity of the secretion has never been estimated. During sleep it is much diminished; and when the eyes are open, the quantity is sufficient to moisten the eyeball, the excess being carried into the nose so gradually that this process is not appreciated. That this drainage of the excess of tears takes place, is shown by cases of obstruction of the nasal duct, when the liquid constantly overflows upon the cheeks, producing considerable inconvenience.


FIG. 262.—*Lachrymal canals, lachrymal sac and nasal canal, opened by their anterior portion* (Sappey).

1, walls of the lachrymal passages, smooth and adherent; 2, 2, walls of the lachrymal sac, presenting delicate folds of the mucous membrane; 3, a similar fold belonging to the nasal mucous membrane.

It is probable that the openings at the puncta lacrymalia take up the lachrymal fluid, like delicate pipettes, this action being aided by the movements in winking, by which, when the lids are closed, the points are compressed and turned backward, opening and drawing in the tears when the lids are opened. It is possible that the lachrymal sac is compressed in the act of winking, by the contractions of the muscle of Horner, and that this, while it empties the sac, may in the subsequent relaxation assist the introduction of liquid from the orbit.

Very little is known with regard to the chemical composition of tears, beyond the analysis made many years ago by Frerichs. According to this observer the following is the composition of the lachrymal secretion:

COMPOSITION OF THE TEARS.

| | | | |
|---|---|---|---|
| Water | 990·60 | to | 987·00 |
| Epithelium | 1·40 | " | 3·20 |
| Albumen | 0·80 | " | 1·00 |
| Sodium chloride, Alkaline phosphates, Earthy phosphates, Mucus, Fat | 7·20 | " | 8·80 |
| | 1,000·00 | | 1,000·00 |

The specific gravity of the tears has never been ascertained. The liquid is perfectly clear, colorless, of a saltish taste and a feebly alkaline reaction. The albumen given in the table is called by some authors, lachrymine, thrænine or dacryoline. This substance, whatever it may be called, resembles mucus in many regards and probably is secreted by the conjunctiva and not by the lachrymal glands. Unlike ordinary mucus, it is coagulated by water.

The secretion of tears is readily influenced through the nervous system. Aside from the increased flow of this secretion from emotional causes, which probably operate through the sympathetic, a hypersecretion almost immediately follows irritation of the mucous membrane of the conjunctiva or of the nose. The same result follows violent muscular effort, laughing, coughing, sneezing etc. The secretion of tears following stimulation of the mucous membrane is reflex.

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## CHAPTER XXIII.

### *AUDITION.*

Auditory (eighth nerve)—General properties of the auditory nerves—Topographical anatomy of the parts essential to the appreciation of sound—The external ear—General arrangement of the parts composing the middle ear—Anatomy of the tympanum—Arrangement of the ossicles of the ear—Muscles of the middle ear—Mastoid cells—Eustachian tube—Muscles of the Eustachian tube—General arrangement of the bony labyrinth—Physics of sound—Noise and musical sounds—Pitch of musical sounds—Musical scale—Quality of musical sounds—Harmonics, or overtones—Resultant tones—Summation tones—Harmony—Discords—Tones by influence—Uses of different parts of the auditory apparatus—Structure of the membrana tympani—Uses of the membrana tympani—Mechanism of the ossicles of the ear—Physiological anatomy of the internal ear—General arrangement of the membranous labyrinth—Liquids of the labyrinth—Distribution of nerves in the labyrinth—Organ of Corti—Uses of different parts of the internal ear—Centres for audition.

IMPRESSIONS of sound are conveyed to the brain by special nerves; but in order that these impressions shall reach these nerves so as to be properly appreciated, a complex accessory apparatus is required, the integrity of which is essential to perfect audition. The study of the arrangement and action of these accessory parts is even more important and is far more intricate than the physiology of the auditory nerves. The auditory nerves conduct impressions of sound, as the optic nerves conduct impressions of light; but there is an elaborate arrangement of parts by which the waves are collected, conveyed to a membrane capable of vibration, and finally carried to the nerves, by which the intensity and the varied qualities of sound are appreciated.

### Auditory (Eighth Nerve).

The origin of the auditory nerve can easily be traced to the floor of the fourth ventricle, where it presents two roots. The external, or superficial root, sometimes called the posterior root, can be seen usually without preparation. It consists of five to seven grayish filaments, which decussate in the median line, and pass outward, winding from the fourth ventricle around the restiform body. The deep root consists of a number of distinct filaments arising from the gray matter of the fourth ventricle, two or three of which pass to the median line, to decussate with corresponding filaments from the opposite side. Filaments from this root have been traced to a gray nucleus in the inferior peduncle of the cerebellum and thence to the white substance of the cerebellum itself. The deep root passes around the restiform body inward, so that this portion of the medulla is encircled by the two roots. Passing from the superior and lateral portion of the medulla oblongata, the trunk of the nerve is applied to the superior and anterior surface of the facial. It then passes around the middle peduncle of the cerebellum, and receives a process from the arachnoid membrane, which envelops it in a common sheath with the facial. It finally penetrates the internal auditory meatus. In its course it receives filaments from the restiform body and possibly from the pons Varolii. Within the meatus the nerve divides into an anterior and a posterior branch, the anterior being distributed to the cochlea, and the posterior, to the vestibule and semicircular canals. The distribution of these branches will be fully described in connection with the anatomy of the internal ear.

The auditory nerves are grayish in color, and their consistence is soft, thus differing from the ordinary cerebro-spinal nerves, and resembling to a certain extent the other nerves of special sense. On the external, or superficial root, is a small, ganglioform enlargement, containing fusiform nerve-cells. The filaments of the trunk of the nerve consist of very large axis-cylinders, surrounded by a medullary sheath, but having no tubular membrane. In the course of these fibres, are found small, nucleated, ganglionic enlargements.

*General Properties of the Auditory Nerves.*—There can be no doubt, as regards the eighth, that it is the only nerve capable of receiving and conveying to the brain the special impressions produced by waves of sound; but it is an important question to determine whether this nerve be endowed also with general sensibility. Analogy with most of the other nerves of special sense would indicate that the auditory nerves are insensible to ordinary impressions; and this view has been sustained by direct experiments. In experiments made by passing electric currents through the ears, some physiologists have thought that auditory sensations were produced; but it is probable that the sensations observed were due to clonic spasm of the stapedius muscle and not to impressions of sound produced by the action of the stimulus upon the auditory nerves. In cases of complete facial paralysis from otitis, in which paralysis of the auditory nerve could be positively excluded, it has not been possible to produce subjective auditory sensations, even by powerful Faradization by means of a catheter passed through the Eustachian tube into the tympanic cavity or by the external meatus (Wreden). In addition there are well established clinical observations which sustain the theory of muscular contraction and are opposed to the idea of impressions of sound produced by direct stimulation of the auditory nerves. The results, then, as regards stimulation of the auditory nerves, have been simply negative. Were it possible to subject these nerves to mechanical or electric stimulation, in the human subject, without involving other parts, it might be possible to arrive at a definite conclusion; but the difficulties in the way of such an experiment have thus far proved insurmountable.

## Topographical Anatomy of the Parts essential to the Appreciation of Sound.

Perfect audition involves the anatomical integrity of a complex apparatus, which, for convenience of anatomical description, may be divided into the external, middle and internal ear.

1. The external ear includes the pinna and the external auditory meatus, and is closed internally by the membrana tympani.

2. The middle ear includes the cavity of the tympanum, or drum, with its boundaries. The parts here to be described are the membrana tympani, the form of the tympanic cavity, its openings, its lining membrane, and the small bones of the ear, or ossicles, with their ligaments, muscles and nerves. The cavity of the tympanum communicates by the Eustachian tube with the pharynx, and it also presents openings into the mastoid cells.

3. The internal ear contains the terminal filaments of the auditory nerve. It includes the vestibule, the three semicircular canals and the cochlea, which together form the labyrinth.

The pinna and the external meatus simply conduct the waves of sound to the tympanum. The parts entering into the structure of the middle ear are accessory, and are analogous in their uses to the refracting media of the eye. Structures contained in the labyrinth constitute the true sensory organ.

*The External Ear.*—The pinna, or auricle, is that portion projecting from the head, which first receives the waves of sound. The outer ridge of the pinna is called the helix. Just within this, is a groove called the fossa of the helix. This fossa is bounded anteriorly by a prominent but shorter ridge, called the antihelix; and above the concha, between the superior portion of the antihelix and the anterior portion of the helix, is a shallow fossa, called the fossa of the antihelix. The deep fossa, immediately surrounding the opening of the meatus, is called the concha. A small lobe projects posteriorly, covering the anterior portion of the concha, which is called the tragus; and the projection at the lower extremity of the antihelix is called the antitragus. The fleshy, dependent portion of the pinna is called the lobule of the ear.

The form of the pinna and its consistence depend upon the presence of fibro-cartilage, which occupies the whole of the external ear except the lobule. The structure of this kind of cartilage has already been described.

The integument covering the ear does not vary much from the integument of the general surface. It is thin, closely attached to the subjacent parts, and possesses small, rudimentary hairs, with sudoriparous and sebaceous glands.

The muscles of the external ear are not important in the human subject; and excluding a few exceptional cases, they are not under the control of the will. The extrinsic muscles are the superior, or attollens, the anterior, or attrahens, and the posterior, or retrahens aurem. In addition there are the six small intrinsic muscles, situated between the ridges upon the cartilaginous surface. The pinna is attached to the sides of the head, by two distinct ligaments and a few delicate, ligamentous fibres.

The external auditory meatus is about an inch and a quarter (31·8 mm.) in length and extends from the concha to the membrana tympani. Its course is somewhat tortuous. Passing from without inward, its direction is at first somewhat upward, turning abruptly over a bony prominence near the middle, from which it has a slightly downward direction, to the membrana tympani. Its general course is from without inward and slightly forward. The inner termination of the canal is the membrana tympani, which is quite oblique, the upper portion being inclined outward, so that the inferior wall of the meatus is considerably longer than the superior.

The walls of the external meatus are partly cartilaginous and fibrous, and partly bony. The cartilaginous and fibrous portion occupies a little less than one-half of the entire length and consists of a continuation of the cartilage of the pinna, with fibrous tissue. The lower two-thirds of this portion of the canal is cartilaginous, the upper third being fibrous. The rest of the tube is osseous and is a little longer and narrower than the cartilaginous portion. Around the inner extremity of the canal, except at its superior portion, is a narrow groove, which receives the greater portion of the margin of the membrana tympani.

The skin of the external meatus is continuous with the integument covering the pinna. It is very delicate, becoming thinner from without inward. In the osseous portion it adheres very closely to the periosteum, and at the bottom of the canal it is reflected over the membrana tympani, forming its outer layer. In the cartilaginous and fibrous portion, are short, stiff hairs, with sebaceous glands attached to their follicles, and the coiled tubes known as the ceruminous glands. The structure of these glands and the properties and composition of the cerumen have already been described in connection with the physiology of the glands of the skin.

*General Arrangement of the Parts composing the Middle Ear.*—Without a very elaborate description, fully illustrated by plates, it is difficult to give a clear idea of the structure and relations of the complex anatomical parts in the middle and the internal ear. Such a minute and purely anatomical description would be out of place in this work, where it is desired only to give such an account of the anatomy as will enable the student to comprehend the physiology of the ear, reserving for special description certain of the most important structures. It will be useful, however, to give a general outline of the different parts, with their names.

The arrangement of the parts constituting the external ear is sufficiently simple. The middle ear presents a narrow cavity (Fig. 263, 11), of irregular shape, situated between the external ear and the labyrinth, in the petrous portion of the temporal bone. The general arrangement of its parts is shown in Fig. 263. The outer wall of the tympanic cavity is formed by the membrana tympani (Fig. 263, 6). This membrane is concave, its concavity looking outward, and oblique, inclining usually at an angle of forty-five degrees with the perpendicular. This angle, however, varies considerably in different individuals. The roof is formed by a thin plate of bone. The floor is bony and is much narrower than the roof. The inner wall, separating the tympanic cavity from the labyrinth, is irregular, presenting several small elevations and foramina. The fenestra ovalis, an ovoid opening near its upper portion, leads to the cavity of the vestibule. This is closed in the natural state by the base of the stapes and its annular ligament. Below is a smaller opening, the fenestra rotunda, which leads to the cochlea. This is closed in the natural state by a membrane called the secondary membrana tympani. In addition the posterior wall presents several small foramina leading to the mastoid cells, which cells are lined by a continuation of the mucous membrane of the tympanic

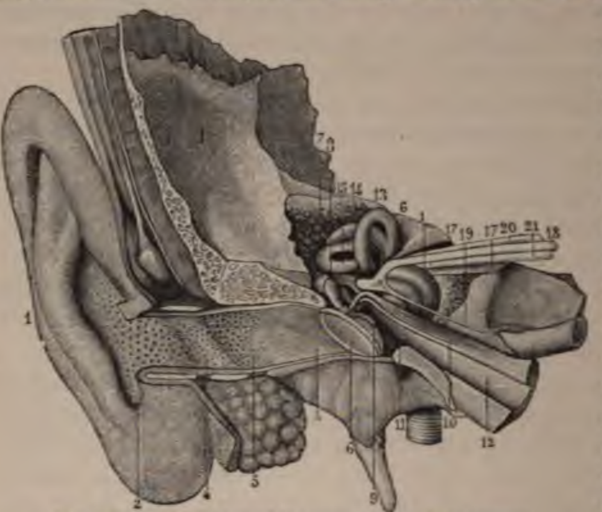


FIG. 263.—*General view of the organ of hearing* (Sappey).

1, pinna; 2, cavity of the concha, on the walls of which are seen the orifices of a great number of sebaceous glands; 3, external auditory meatus; 4, angular projection formed by the union of the anterior portion of the concha with the posterior wall of the auditory canal; 5, openings of the ceruminous glands, the most internal of which form a curved line which corresponds with the beginning of the osseous portion of the external meatus; 6, membrana tympani and the elastic fibrous membrane which forms its border; 7, anterior portion of the incus; 8, malleus; 9, handle of the malleus, applied to the internal surface of the membrana tympani, which it draws inward toward the projection of the promontory; 10, tensor tympani muscle, the tendon of which is reflected at a right angle, to become attached to the superior portion of the handle of the malleus; 11, tympanic cavity; 12, Eustachian tube, the internal, or pharyngeal extremity of which has been removed by a section perpendicular to its curve; 13, superior semicircular canal; 14, posterior semicircular canal; 15, external semicircular canal; 16, cochlea; 17, internal auditory canal; 18, facial nerve; 19, large petrosal branch, given off from the ganglioform enlargement of the facial and passing below the cochlea, to go to its distribution; 20, vestibular branch of the auditory nerve; 21, cochlear branch of the auditory nerve.

cavity. The tympanic cavity also presents an opening leading to the Eustachian tube, and a small foramen which gives passage to the tendon of the stapedius muscle. The Eustachian tube extends from the upper part of the pharynx to the tympanum.

The small bones of the ear are three in number; the malleus, the incus, and the stapes, forming a chain and connected together by ligaments (D, Fig. 264). These bones are situated in the upper part of the tympanic cavity. The handle of the malleus (A, 2, Fig. 264) is closely attached to the membrana tympani, and the long process (A, 3, Fig. 264) is attached to the Glasserian fissure of the temporal bone. The malleus is articulated with the incus. The incus (B, Fig. 264) is connected with the posterior wall of the tympanic cavity, near the openings of the mastoid cells. It is articulated with the malleus, and by the extremity of its long process (B, 2, Fig. 264), with the stapes. The stapes (C, Fig. 264) is the most internal bone of the middle ear. It is articulated by its smaller extremity with the long process of the incus. Its base is oval (C′, Fig. 264) and with its annular ligament, is applied to the fenestra ovalis. The direction of the stapes is nearly at a right angle with the long process of the incus, in the natural state (8, Fig. 265). Some anatomists describe a fourth bone as existing between the long process of the incus and the stapes, but this is seldom distinct, usually being united either with the incus or with the stapes.

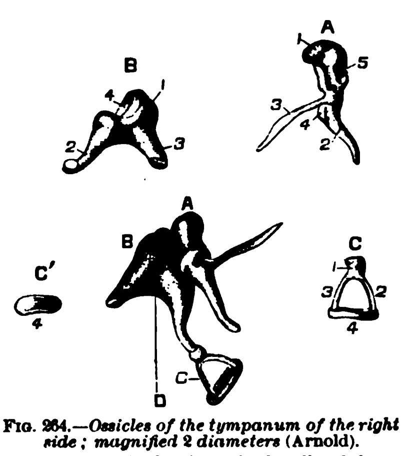


FIG. 264.—*Ossicles of the tympanum of the right side; magnified 2 diameters* (Arnold).

A, malleus; 1, its head; 2, the handle; 3, long, or slender process; 4, short process; B, incus; 1, its body; 2, the long process, with the orbicular process; 3, short, or posterior process; 4, articular surface, receiving the head of the malleus; C, stapes; 1, head; 2, posterior crus; 3, anterior crus; 4, base; C′, base of the stapes; D, the three bones in their natural connection, as seen from the outside; A, malleus; B, incus; C, stapes.

There are two well defined muscles connected with the ossicles of the middle ear. One of these is attached to the malleus, and the other, to the stapes. The so-called laxator tympani probably is not composed of muscular fibres and should not be enumerated with the muscles of the tympanum.

The larger of the two muscles is the tensor tympani. Its fibres arise from the cartilaginous portion of the Eustachian tube, the spinous process of the sphenoid bone and the adjacent portion of the temporal. From this origin it passes backward, almost horizontally, to the tympanic cavity. In front of the fenestra ovalis it turns nearly at a right angle over a bony process, and its tendon is inserted into the handle of the malleus, at its inner surface near the root. The tendon is very delicate, and the muscular portion is about half an inch (12·7 mm.) in length (10, Fig. 263). The muscle and its tendon are enclosed in a distinct, fibrous sheath. The action of this muscle is to draw the handle of the malleus inward, pressing the base of the stapes against the membrane of the fenestra ovalis and producing tension of the membrana tympani. The fibres of this, and of all the muscles of the middle ear, are of the striated variety. The tensor tympani is supplied with motor filaments from the otic ganglion, which are probably derived from the facial nerve.

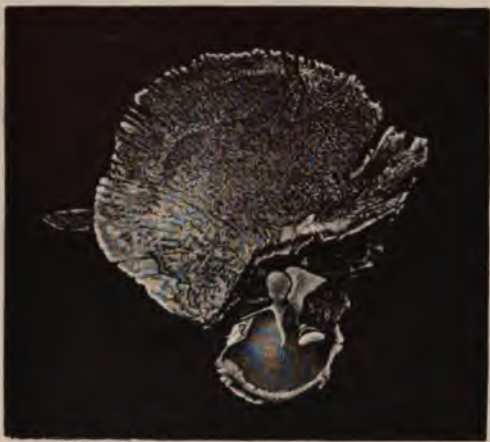

FIG. 265.—*The right temporal bone, the petrosal portion removed, showing the ossicles seen from within.* From a photograph (Rüdinger).

4, the incus, the short process of which is directed nearly in a horizontal direction backward; 5, the long process of the incus, free in the tympanic cavity, articulated with the stapes; 6, the malleus, articulated with the incus; 7, the long process of the malleus, in the Glasserian fissure; 8, the stapes, articulated with the incus. This is drawn somewhat outward; otherwise the base of the stapes alone would be visible. This figure shows the handle of the malleus, attached to the membrana tympani.

The stapedius muscle is situated in the descending portion of the acquæductus Fallopii and in the cavity of the pyramid on the posterior wall of the tympanic cavity. Its tendon emerges from a foramen at the summit of the pyramid. In the canal in which this muscle is lodged, its direction is vertical. At the summit of the pyramid, it turns at nearly a right angle, its tendon passing horizontally forward, to be attached to the head of the stapes. Like the other muscles of the ear, this is enveloped in a fibrous sheath. Its action is to draw the head of the stapes backward, relaxing the membrana tympani. This muscle receives filaments from the facial nerve, by a distinct branch, the tympanic.

The posterior wall of the tympanic cavity presents several foramina, which open directly into a number of irregularly shaped cavities communicating freely with each other in the mastoid process of the temporal bone. These are called the mastoid cells. They are lined by a continuation of the mucous membrane of the tympanum. There is under certain conditions a free circulation of air between the pharynx and the cavity of the tympanum, through the Eustachian tube, and from the tympanum to the mastoid cells.

The Eustachian tube (12, Fig. 263) is partly bony and partly cartilaginous. Following its direction from the tympanic cavity, it passes forward, inward and slightly downward. Its entire length is about an inch and a half (38·1 mm.). Its caliber gradually contracts from the tympanum to the spine of the sphenoid, and from this constricted portion it gradually dilates to its opening into the pharynx, the entire canal presenting the appearance of two cones. The osseous portion extends from the tympanum to the spine of the sphenoid bone. The cartilaginous portion is an irregularly triangular cartilage, bent upon itself above, forming a furrow with its concavity presenting downward and outward. The fibrous portion occupies about half of the tube beyond the osseous portion, and completes the canal, forming its inferior and external portion. In its structure the cartilage of the Eustachian tube is intermediate between the hyaline and the fibro-cartilage.

The circumflexus, or tensor palati muscle, which has already been described in connection with deglutition, is attached to the anterior margin, or the hook of the cartilage. The attachments of this muscle have been accurately described by Rüdinger, who called it the dilator of the tube.

The action of certain of the muscles of deglutition dilates the pharyngeal opening of the Eustachian tube. If the mouth and nostrils be closed and several repeated acts of deglutition be made, air is drawn from the tympanic cavity, and the atmospheric pressure renders the membrane of the tympanum tense, increasing its concavity. By one or two lateral movements of the jaws, the tube is opened, the pressure of air is equalized and the ear returns to its normal condition. The nerves animating the dilator tubæ come from the pneumogastric and are derived from the spinal accessory.

A smooth, mucous membrane forms a continuous lining for the Eustachian tube, the cavity of the tympanum and the mastoid cells. In all parts it is closely adherent to the subjacent tissues, and in the cavity of the tympanum it is very thin. In the cartilaginous portion of the Eustachian tube there are mucous glands, which are most abundant near the pharyngeal orifice and gradually diminish in number toward the osseous portion, in which there are no glands. Throughout the tube the surface of the mucous membrane is covered with conoidal cells of ciliated epithelium. The mucous membrane of the tympanic cavity is very thin, consisting of little more than epithelium and a layer of connective tissue. It lines the walls of the cavity and the inner surface of the membrana tympani, is prolonged into the mastoid cells and covers the ossicles and those portions of the muscles and tendons which pass through the tympanum. On the floor of the tympanic cavity and on its anterior, inner and posterior walls, the epithelium is of the conoidal, ciliated variety. On the promontory, roof, ossicles and muscles, the cells are of the pavement-variety and not ciliated, the transition from one form to the other being gradual. The entire mucous membrane contains lymphatics, a plexus of nerve-fibres and nerve-cells, with some peculiar cells, the physiology of which is not understood.

The above is merely a general sketch of the physiological anatomy of the middle ear, and it will not be necessary to treat more fully of the cavity of the tympanum, the mastoid cells or the Eustachian tube, except as regards certain points in their physiology. The minute anatomy of the membrana tympani and the articulations of the ossicles can be more conveniently considered in connection with the physiology of these parts.

*General Arrangement of the Bony Labyrinth.*—The internal portion of the auditory apparatus is contained in the petrous portion of the temporal bone. It consists of an irregular cavity, called the vestibule, the three semicircular canals (13, 14, 15, Fig. 263) and the cochlea (16, Fig. 263). The general arrangement of these parts *in situ* and their relations to the adjacent structures are shown in Fig. 263. Fig. 266, showing the bony labyrinth isolated, is from a photograph in Rüdinger's atlas.

The vestibule is the central chamber of the labyrinth, communicating with the tympanic cavity by the fenestra ovalis, which is closed in the natural state by the base of the stapes. This is the central, ovoid opening shown in Fig. 266. The inner wall of the vestibule presents a round depression, the fovea hemispherica, perforated by a number of small foramina, through which pass nervous filaments from the internal auditory meatus. Behind this depression is the opening of the aqueduct of the vestibule. In the posterior wall of the vestibule are five small, round openings leading to the semicircular canals, with a larger opening below, leading to the cochlea.

The general arrangement of the semicircular canals is shown in Fig. 266 (6, 7, 8, 9, 10, 11, 12).

The arrangement of the cochlea, the anterior division of the labyrinth, is shown in Fig. 266 (1, 3, 4). This is a spiral canal, about an inch and a half (38·1 mm.) long, and one-tenth of an inch (2·5 mm.) wide at its beginning, gradually tapering to the apex, and making in its course, two and a half turns. Its anterior presents a central pillar, around which winds a spiral lamina of bone. The fenestra rotunda (2, Fig. 266), closed in the natural state by a membrane (the secondary membrana tympani), lies between the lower portion of the cochlea and the cavity of the tympanum.


FIG. 266.—*The left bony labyrinth of a new-born child, forward and outward view.* From a photograph (Rüdinger).

1, the wide canal, the beginning of the spiral canal of the cochlea; 2, the fenestra rotunda; 3, the second turn of the cochlea; 4, the final half-turn of the cochlea; 5, the border of the bony wall of the vestibule, situated between the cochlea and the semicircular canals; 6, the superior, or sagittal semicircular canal; 7, the portion of the semicircular canal bent outward; 8, the posterior, or transverse semicircular canal; 9, the portion of the posterior connected with the superior semicircular canal; 10, point of junction of the superior and the posterior semicircular canals; 11, the ampulla ossea externa; 12, the horizontal, or external semicircular canal. The explanation of this figure has been modified and condensed from Rüdinger.

What is called the membranous labyrinth is contained within the bony parts just described. Some of the anatomical points connected with its structure and the distribution and connections of the auditory nerve have direct and important relations to the physiology of hearing, while many are of purely anatomical interest. Such facts as bear directly upon physiology will be considered fully in connection with the uses of the internal ear.

## Physics of Sound.

The sketch just given of the general anatomical arrangement of the auditory apparatus conveys a general idea of the uses of the different parts of the ear. The waves of sound must be transmitted to the terminal extremities of the auditory nerve in the labyrinth. These waves are collected by the pinna, are conducted to the membrana tympani through the external auditory meatus, produce vibrations of the membrana tympani, are conducted by the chain of ossicles to the openings in the labyrinth and are communicated through the fluids of the labyrinth to the ultimate nervous filaments. The free passage of air through the external meatus and the communications of the cavity of the tympanum with the mastoid cells, and by the Eustachian tube, with the pharynx, are necessary to the proper vibration of the membrana tympani; the integrity of the ossicles and of their ligaments and muscles is essential to the proper conduction of sound to the labyrinth; the presence of liquid in the labyrinth is a condition essential to the conduction of the waves to the filaments of distribution of the auditory nerves; and finally, from the labyrinth, the nerves pass through the internal auditory meatus, to the auditory centre in the brain, where the auditory impressions are appreciated.

Most of the points in acoustics which are essential to the comprehension of the physiology of audition are definitely settled. The theories of the propagation of sound involve wave-action, concerning which there is no dispute among physicists. For the conduction of sound a ponderable medium is essential; and it is not necessary, as in the case of the undulatory theory of light, to assume the existence of an imponderable ether. The human ear, though perhaps not so acute as the auditory apparatus of some of the inferior animals, not only appreciates irregular waves, such as produce noise as distinguished from sounds called musical, but is capable of distinguishing regular waves, as in simple, musical sounds, and harmonious combinations.

In music certain successions of regular sounds are agreeable to the ear and constitute what is called melody. Again, there is appreciation, not only of the intensity of sounds, both noisy and musical, but of pitch and different qualities, particularly in music. Still farther, musical notes may be resolved into certain invariable component parts, such as the octave, the third, fifth etc. These components of what were formerly supposed to be simple sounds —which may be isolated by artificial means, to be described farther on—are called tones; while the sounds themselves, produced by the union of the different tones, are called notes, which may themselves be combined to form chords.

The quality of musical sounds may be modified by the simultaneous production of others which correspond to certain of the components of the predominating note. For example, if there be added to a single note, the third, fifth and octave, the result is a major chord, the sound of which is very different from that of a single note or of a note with its octave. If the third be diminished by a semitone, there is a different quality, which is peculiar to minor chords. In this way a great variety of musical sounds may be made upon a single instrument, as the piano; and by the harmonious combinations of the notes of different instruments and of different registers of the human voice, as in choral and orchestral compositions, shades of effect, almost innumerable, may be produced. The modification of sounds in this way constitutes harmony; and an educated ear not only experiences pleasure from these musical combinations, but can distinguish their different component parts.

A chord may convey to the ear the sensation of completeness in itself or it may lead to a succession of notes before this sense of completeness is attained. Different chords of the same key may be made to follow each other, or by transition-notes, may pass to the chords of other keys. Each key has its fundamental note, and the transition from one key to another, in order to be agreeable to the ear, must be made in certain ways. These regular transitions constitute modulation. The ear becomes fatigued by long successions of notes or chords always in one key, and modulation is essential to the enjoyment of elaborate musical compositions; otherwise the notes would not only become monotonous, but their correct appreciation would be impaired, as the appreciation of colors becomes less distinct after looking for a long time at an object presenting a single vivid tint.

*Laws of Sonorous Vibrations.*—Sound is produced by vibrations in a ponderable medium; and the sounds ordinarily heard are transmitted to the ear by means of vibrations of the atmosphere. A simple and very common illustration of this fact is afforded by the experiment of striking a bell carefully arranged *in vacuo.* Although the stroke and the vibration can readily be seen, there is no sound; and if air be gradually introduced, the sound will become appreciable, and progressively more intense as the surrounding medium is increased in density. The oscillations of sound are to and fro in the direction of the line of conduction and are said to be longitudinal. In the undulatory theory of light, the vibrations are supposed to be at right angles to the line of propagation, or transversal. A complete oscillation to and fro is called a sound-wave.

It is evident that vibrating bodies may be made to perform and impart to the atmosphere oscillations of greater or less amplitude. The intensity of sound is in proportion to the amplitude of the vibrations. In a vibrating body capable of producing a definite number of waves of sound in a second, it is evident that the greater the amplitude of the wave, the greater is the velocity of the particles thrown into vibration. It has been ascertained that there is an invariable mathematical relation between the intensity of sound, the velocity of the conducting particles and the amplitude of the waves; and this is expressed by the formula, that the intensity is proportional to the square of the amplitude. It is evident, also, that the intensity of sound is diminished by distance. The sound, as the waves recede from the sonorous body, becomes distributed over an increased area. The propagation of sound has been reduced also to the formula, that the intensity diminishes in proportion to the square of the distance.

Sonorous vibrations are subject to many of the laws of reflection of light. Sound may be absorbed by soft and non-vibrating surfaces, in the same way that certain surfaces aborb the rays of light. By carefully arranged convex surfaces, the waves of sound may readily be collected to a focus. These laws of the reflection of sonorous waves explain echoes and the conduction of sound by confined strata of air, as in tubes. To make the parallel between sonorous and luminous transmission more complete, it has been ascertained that the waves of sound may be refracted to a focus, by being made to pass through an acoustic lens, as a balloon filled with carbon dioxide. The waves of sound may also be deflected around solid bodies, when they produce what have been called by Tyndall, shadows of sound.

Any one observing the sound produced by the blow of an axe can note the fact that sound is transmitted with much less rapidity than light. At a short distance the view of the body is practically instantaneous; but there is a considerable interval between the blow and the sound. This interval represents the velocity of sonorous conduction. This fact is also illustrated by the interval between a flash of lightning and the sound of thunder. The velocity of sound depends upon the density and elasticity of the conducting medium. The rate of conduction of sound, by atmospheric air at the freezing-point of water, is about 1,090 feet (332 metres) per second. This rate presents comparatively slight variations for the different gases, but it is very much more rapid in liquids and in solids.

*Noise and Musical Sounds.*—There is a well defined physical as well as an æsthetic distinction between noise and music. Taking as examples, single sounds, a sound becomes noise when the air is thrown into confused and irregular vibrations. A noise may be composed of musical sounds, when these are not in accord with each other, and sounds called musical are not always entirely free from discordant vibrations. A noise possesses intensity, varying with the amplitude of the vibrations, and it may have different qualities depending upon the form of its vibrations. A noise may be called dull, sharp, ringing, metallic, hollow etc., these terms expressing qualities that are readily understood. A noise may also be called sharp or low in pitch, as the rapid or slow vibrations predominate, without answering the requirements of musical sounds.

A musical sound consists of vibrations following each other at regular intervals, provided that the succession of waves be not too slow or too rapid. When the vibrations are too slow, there is an appreciable succession of impulses, and the sound is not musical. When they are too rapid, the sound is excessively sharp, but it is painfully acute and has no pitch that can be accurately determined by the auditory apparatus. Such sounds may be occasionally employed in musical compositions, but in themselves they are not strictly musical.

Musical sounds have the characters of duration, intensity, pitch and quality. Duration depends simply upon the length of time during which the vibrating body continues in action. Intensity depends upon the amplitude of the vibrations, and it has no relation whatsoever to pitch. Pitch depends absolutely upon the rapidity of the regular vibrations, and quality, upon the combinations of different notes in harmony, the character of the harmonics of fundamental tones and the form of the vibrations.

*Pitch of Musical Sounds.*—Pitch depends upon the number of vibrations. A musical sound may be of greater or less intensity; it may at first be quite loud and gradually die away; but the number of vibrations in a definite note is invariable, be it weak or powerful. The rapidity of the conduction of sound does not vary with its intensity or pitch, and in the harmonious combination of the sounds of different instruments, be they high or low in pitch, intense or feeble, it is always the same in the same conducting medium. Distinct musical notes may present a great variety of qualities, but all notes of the same pitch have absolutely equal rates of vibration. Notes equal in pitch are said to be in unison. An educated ear can distinguish slight differences in pitch in ordinary musical notes; but this power of appreciation of pitch is restricted within well defined limits, which vary slightly in different individuals. According to Helmholtz, the range of sounds that can be legitimately employed in music is between 40 and 4,000 vibrations in a second, embracing about seven octaves. In an orchestra the double bass gives the lowest note, which has 40·25 vibrations in a second, and the highest note, given by the small flute, has 4,752 vibrations. In grand organs there is a pipe which gives a note of 16·5 vibrations, and the deepest note of modern pianos has 27·5 vibrations; but delicate shades of pitch in these low notes are not appreciable to most persons. Sounds above the limits just indicated are painfully sharp, and their pitch can not be exactly appreciated by the ear.

*Musical Scale.*—A knowledge of the relations of different notes to each other lies at the foundation of the science of music; and without a clear idea of certain of the fundamental laws of music, it is impossible to thoroughly comprehend the mechanism of audition.

It requires very little cultivation of the ear to enable one to comprehend the fact that the successions and combinations of notes must obey certain fixed laws; and long before these laws were subjects of mathematical demonstration, the relations of the different notes of the scale were established, merely because certain successions and combinations were agreeable to the ear, while others were discordant and apparently unnatural.

The most convenient sounds for study are those produced by vibrating strings, and the phenomena here observed are essentially the same for all musical sounds; for it is by means of vibrations communicated to the air that the waves of sound find their way to the auditory apparatus. Take, to begin with, a string vibrating 48 times in a second. If this string be divided into two equal parts, each part will vibrate 96 times in a second. The note thus produced is the octave, or the 8th of the primary note, called the 8th, because the natural scale contains eight notes, of which the first is the lowest, and the last, the highest. The half may be divided again, producing a second octave, and so on, within the limits of appreciation of musical sounds. If the string be divided so that $\frac{2}{3}$ of its length will vibrate, there are 72 vibrations in a second, and this note is the 5th in the scale. If the string be divided again, so as to leave $\frac{4}{5}$ of its length, there are 60 vibrations, which give the 3d note in the scale. These are the most natural subdivisions of the note; and the 1st, 3d, 5th and 8th, when sounded together, make what is known as the common major chord. Three-fourths of the length of the original string make 64 vibrations, and give the 4th note in the scale. With $\frac{8}{9}$ of the string, there are 54 vibrations, and the note is the 2d in the scale. With $\frac{3}{5}$ of the string, there are 80 vibrations, or the 6th note in the scale. With $\frac{8}{15}$ of the string, there are 90 vibrations, or the 7th note in the scale. The original note, which may be called C, is the key-note, or the tonic. In this scale, which is called the natural, or diatonic, there is a regular mathematical progression from the 1st to the 8th. This is called the major key. Melody consists in an agreeable succession of notes, which may be assumed, for the sake of simplicity, to be pure. In a simple melody every note must be one of those in the scale. When a different note is sounded, the melody passes into a key which has a different fundamental note, or tonic, with a different succession of 3ds, 5ths etc. Every key, therefore, has its 1st, 3d, 5th and 8th, as well as the intermediate notes. If a note formed by a string $\frac{5}{6}$ the length of the tonic instead of $\frac{4}{5}$, be substituted for the major 3d, the key is converted into the minor. The minor chord, consisting of the 1st, the diminished 3d, the 5th and the 8th, is perfectly harmonious, but it has a quality quite different from that of the major chord. The notes of a melody may progress in the minor key as well as in the major. Taking the small numbers of vibrations merely for convenience, the following is the mode of progression in the natural scale, which may be assumed to be the scale of C major:

| | 1st. | 2d. | 3d. | 4th. | 5th. | 6th. | 7th. | 8th. |
|---|---|---|---|---|---|---|---|---|
| Note | C | D | E | F | G | A | B | C |
| Lengths of the string | 1 | $\frac{8}{9}$ | $\frac{4}{5}$ | $\frac{3}{4}$ | $\frac{2}{3}$ | $\frac{3}{5}$ | $\frac{8}{15}$ | $\frac{1}{2}$ |
| Number of vibrations | 48 | 54 | 60 | 64 | 72 | 80 | 90 | 96 |

The intervals between the notes of the scale, it is seen, are not equal. The smallest, between the 3d and 4th and the 7th and 8th, are called semitones. The other intervals are either full perfect tones or small perfect tones. Although there are semitones, not belonging to the key of C, between C and D, D and E, F and G, G and A, and A and B, these intervals are not all composed of exactly the same number of vibrations; so that, taking the notes on a piano, with D as the tonic, the 5th would be A. It is assumed that D has 54 vibrations, and A, 80, giving a difference of 26. With C as the tonic and G as the fifth, there is a difference of 24. It is on account of these differences in the intervals, that each key in music has a more or less peculiar and distinctive character.

Even in melody, and still more in harmony, in long compositions, the ear becomes fatigued by a single key, and it is necessary, in order to produce the most pleasing effects, to change the tonic, by what is called modulation, returning afterward to the original key.

*Quality of Musical Sounds.*—Nearly all musical sounds, which seem at first to be simple, can be resolved into certain well defined constituents; but with the exception of the notes of great stopped pipes in the organ, there are few absolutely simple sounds used in music. These simple sounds are pure, but are of an unsatisfactory quality and wanting in richness. Almost all other musical sounds have a fundamental tone, which is at once recognized; but this tone is accompanied by harmonics caused by secondary vibrations of subdivisions of the sonorous body. The number, pitch and intensity of these harmonic, or aliquot vibrations affect what is called the quality, or timbre of musical notes, by modifying the form of the sonorous waves. A string vibrating a certain number of times in a second, if the vibrations were absolutely simple, would produce, according to the laws of vibrating bodies, a simple, musical tone; but as the string subdivides itself into different portions, one of which gives the 3d, another, the 5th, and so on, of the fundamental tone, it is evident that the form of the vibrations must be considerably modified, and with these modifications in form, the quality, or timbre of the note is changed.

From what has just been stated, it follows that nearly all musical notes consist, not only of a fundamental sound, but of harmonic vibrations, subordinate to the fundamental and qualifying it in a particular way. These harmonics may be feeble or intense; certain of them may predominate over others; some that are usually present may be eliminated; and in short, there may be a great diversity in their arrangement, and thus the timbre may present an infinite variety. This is one of the elements entering into the composition of notes, and it affords a partial explanation of quality.

Another element in the quality of notes depends upon their re-enforcement by resonance. The vibrations of a stretched string not connected with a resonant body are almost inaudible. In musical instruments the sound is taken up by some mechanical arrangement, as the sound-board of the organ, piano, violin, harp or guitar. In the violin, for example, the sweetness of the notes depends chiefly upon the construction of the resonant part of the instrument, and but little upon the strings themselves, which latter are frequently changed; and the same is true of the human voice.

In addition to the harmonic tones of sonorous bodies, various discordant sounds are generally present, which modify the timbre, producing, usually, a certain roughness, such as the grating of a violin-bow, the friction of the columns of air against the angles in wind-instruments, etc. All of these conditions have their effect upon the quality of tones; and these discordant sounds may exist in infinite number and variety. These sounds are composed of irregular vibrations and consequently are inharmonious. Nearly all notes that are spoken of in general terms as musical are composed of musical, or harmonic, aliquot tones with the discordant elements to which allusion has just been made.

Aside from the relations of the various component parts of musical notes, the quality depends largely upon the form of the vibrations. To quote the words of Helmholtz, "the more uniformly rounded the form of the wave, the softer and milder is the quality of the sound. The more jerking and angular the wave-form, the more piercing the quality. Tuning-forks, with their rounded forms of wave, have an extraordinarily soft quality; and the qualities of sound generated by the zither and violin resemble in harshness the angularity of their wave-forms."

*Harmonics, or Overtones.*—As before stated, nearly all sounds are composite, but some contain many more aliquot, or secondary vibrations than others. The notes of vibrating strings are peculiarly rich in harmonics, and these may be used for illustration, remembering that the phenomena here observed have their analogies in nearly all varieties of musical sounds. If a stretched string be made to vibrate, the secondary tones, which qualify the fundamental, are called harmonics, or overtones.

While it is difficult at all times to distinguish by the ear the individual overtones of vibrating strings, their existence can be demonstrated by certain simple experiments. Take, for example, a string, the fundamental tone of which is C. If this string be damped with a feather at one-fourth of its length and a violin-bow be drawn across the smaller section, not only the fourth part of the string across which the bow is drawn is made to vibrate, but the remaining three-fourths; and if little riders of paper be placed upon the longer segment at distances equal to one-fourth of the entire string, they will remain undisturbed, while riders placed at any other points on the string will be thrown off. This experiment shows that the three-fourths of the string have been divided. This may be illustrated by connecting one end of the string with a tuning-fork. When this is done and the string is brought to the proper degree of tension, it will first vibrate as a whole, then, when a little tighter, will spontaneously divide into two equal parts, and under increased tension, into three, four, and so on. By damping a string with the light touch of a feather, it is possible to suppress the fundamental tone and bring out the overtones, which exist in all vibrating strings but are usually concealed by the fundamental. The points which mark the subdivisions of the string into segments of secondary vibrations are called nodes. When the string is damped at its centre, the fundamental tone is quenched and there are overtones an octave above; damping it at a distance of one-fourth, there is the second octave above, and so on. When the string is damped at a distance of one-fifth from the end, the four-fifths sound the 3d of the fundamental, with the second octave of the 3d. If it be damped at a distance of two-thirds, there is the 5th of the fundamental, with the octave of the 5th. Every vibrating string thus possesses a fundamental tone and overtones. Qualifying the fundamental there is first, as the most simple, a series of octaves; next, a series of 5ths of the fundamental and their octaves; and next, a series of 3ds. These are the most powerful overtones, and they form the common chord of the fundamental; but they are so far concealed by the greater intensity of the fundamental, that they can not easily be distinguished by the unaided ear, unless the fundamental be quenched in some way. In the same way the harmonic 5ths and 3ds overpower other overtones; for the string is subdivided again and again into overtones, which are not harmonious like the notes of the common chord of the fundamental.

The presence of overtones, resultant tones and additional tones, which latter will be described hereafter, can be demonstrated, without damping the strings, by resonators. It is well known that if a glass tube, closed at one end, which contains a column of air of a certain length, be brought near a resounding body emitting a note identical with that produced by the vibrations of the column of air, the air in the tube will resound in consonance with the note, while no other note will have this effect. The resonators of Helmholtz are constructed upon this principle. A glass globe or tube (Fig. 267) is constructed so as to produce a certain note. This has a larger opening (a) and a smaller opening (b), which latter is fitted in the ear by warm sealing-wax, the other ear being closed. When the proper note is sounded, it is re-enforced by the resonator and is greatly increased in intensity, while all other notes are heard very faintly. By using resonators graduated to the musical scale, it is easy to analyze a note and distinguish its overtones. The resonators of Helmholtz, which are open at the larger extremity, are much more delicate than those in which this is closed by a membrane.

A very striking and instructive point in the present discussion is the following: All the overtones are produced by vibrations of divisions of the string, included between the comparatively still points, called nodes; and if a string be thrown into vibration by plucking or striking it at one of these nodal points, the overtones which vibrate from this node at a fixed point are abolished. It is readily understood that when a string is plucked at any point, it will vibrate so vigorously at this point that no node can be formed. This fact has long been recognized by practical musicians, although many are probably unacquainted with its scientific explanation. Performers upon stringed instruments habitually attack the strings near their extremities. In the piano, where the strings may be struck at almost any point, the hammers are placed at a distance of $\frac{1}{7}$ to $\frac{1}{9}$ of the length of the strings, from their extremities; and it has been ascertained by experience that this arrangement gives the richest notes. The nodes formed at these points would produce the 7ths and 9ths as overtones, which do not belong to the perfect major chord, while the nodes for the harmonious overtones are undisturbed. The reason, then, why the notes

FIG. 267.—*Resonators of Helmholtz.*

are richer and more perfect when the strings are attacked at this point, is that the harmonious overtones are full and perfect, and certain of the discordant overtones are suppressed.

When two harmonious notes are produced under favorable conditions, one can hear, in addition to the two sounds, a sound differing from both and much lower than the lower of the two. This sound is too low for a harmonic, and it has been called a resultant tone. The formation of a new sound by combining two sounds of different pitch is analogous to the blending of colors in optics, except that the primary sounds are not lost. The laws of the production of these resultant sounds are very simple. When two notes in harmony are sounded, the resultant tone is equal to the difference between the two primaries. For example, C, with 48 vibrations, and its 5th, with 72 vibrations in a second, give a resultant tone equal to the difference, which is 24 vibrations, and it is consequently the octave below C. These resultant tones are very feeble as compared with the primary tones, and they can be heard under only the most favorable experimental conditions. In addition to these sounds, Helmholtz has discovered sounds, even more feeble, which he calls additional, or summation tones. The value of these is equal to the sum of vibrations of the primary tones. For example, C (48) and its 5th (72) would give a summation tone of 120 vibrations, or the octave of the 3d; and C (48) with its 3d (60) would give 108 vibrations, the octave of the 2d. These tones can be distinguished by means of resonators.

It is thus seen that musical sounds are complex. With single sounds there is an infinite variety and number of harmonics, or overtones, and in chords there are series of resultants, which are lower than the primary notes, and series of additional, or summation tones, which are higher; but both the resultant and the summation tones bear exact mathematical relations to the primary notes of the chord.

*Harmony.*—Overtones, resultant tones and summation tones of strings have been discussed rather fully, for the reason that in studying the physiology of audition, it will be seen that the ear is capable of recognizing single sounds or successions of single sounds; but at the same time certain combinations of sounds are appreciated and are even more agreeable than those which are apparently produced by simple vibrations. Combinations of tones which thus produce an agreeable impression are called harmonious. They seem to become blended with each other into a complete sound of peculiar quality, all of the different vibrations entering into their composition being simultaneously appreciated by the ear. The blending of tones which bear to each other certain mathematical relations is called harmony; but two or more tones, though each one be musical, are not necessarily harmonious. The most prominent overtone, except the octave, is the 5th, with its octaves, and this is called the dominant. The next is the 3d, with its octaves. The other overtones are comparatively feeble. Reasoning, now, from a knowledge of the relations of overtones, it might be inferred that the re-enforcement of the 5th and 3d by other notes bearing similar relations to the tonic would be agreeable. This is the fact, and it was ascertained empirically long before the pleasing impression produced by such combinations was explained mathematically.

It is a law in music that the more simple the ratio between the number of vibrations in two sounds, the more perfect is the harmony. The simplest relation, of course, is 1 : 1, when the two sounds are said to be in unison. The next in order is 1 : 2. In sounding C and its 8th, for example, there are 48 vibrations of one to 96 of the other. These sounds can produce no discord, because the waves never interfere with each other, and the two sounds can be prolonged indefinitely, always maintaining the same relations. The combined impression is therefore continuous. The next in order is the 1st and 5th, their relations being 2 : 3. In other words, with the 1st and 5th, for two waves of the 1st there are three waves of the 5th. The two sounds may thus progress indefinitely, for the waves coincide for every second wave of the 1st and every third wave of the 5th. The next in order is the 3d. The 3d of C has the 8th of C for its 5th, and the 5th of C for its minor 3d. The 1st, 3d, 5th and 8th form the common major chord; and the waves of each tone blend with each other at such short intervals of time that the ear experiences a continuous impression, and no discord is appreciated. This explanation of the common major chord illustrates the law that the smaller the ratio of vibration between different tones, the more perfect is their harmony. Sounded with the 1st, the 4th is more harmonious than the 3d; but its want of harmony with the 5th excludes it from the common chord. The 1st, 4th and 8th are harmonious, but to make a complete chord the 6th must be added.

*Discords.*—A knowledge of the mechanism of simple accords leads naturally to a comprehension of the rationale of discords. The fact that certain combinations of musical notes produce a disagreeable impression was ascertained empirically, with no knowledge of the exact cause of the dissonance; but the mechanism of discord may now be regarded as settled.

The sounds produced by two tuning-forks giving precisely the same number of vibrations in a second are in perfect unison. If one of the forks be loaded with a bit of wax, so that its vibrations are slightly reduced, and if both be put in vibration at the same instant, there is discord. Taking the illustration given by Tyndall, it may be assumed that one fork has 256, and the other, 255 vibrations in a second. While these two forks are vibrating, one is gradually gaining upon the other; but at the end of half a second, one will have made 128 vibrations, while the other will have made 127½. At this point the two waves are moving in exactly opposite directions; and as a consequence, the sounds neutralize each other, and there is an instant of silence. The perfect sounds, as the two forks continue to vibrate, are thus alternately re-enforced and diminished, and this produces what is known in music as beats. As the difference in the number of vibrations in a second is one, the instants of silence occur once in a second; and in this illustration the beats occur once a second. Unison takes place when two sounds can follow each other indefinitely, their waves blending perfectly; and dissonance is marked by successive beats, or pulses. If the forks be loaded so that one will vibrate 240 times in a second, and the other 234, there will be six times in a second when the interference will be manifest; or in other words in $\frac{1}{6}$ of a second, one fork will make 40 vibrations, while the other is making 39. This will give 6 beats in a second. From these experiments the law may be deduced, that the number of beats produced by two tones not in harmony is equal to the difference between the two rates of vibration. An analogous interference of undulations is observed in optics, when waves of light are made to interfere and produce darkness.

It is evident that the number of beats will increase as two discordant notes are produced higher and higher in the scale. According to Helmholtz, the beats can be recognized up to 132 in a second. Beyond that point they become confused, and there is only a general sensation of dissonance. Beats, then, are due to interference of sound-waves. There is no interference of the waves of tones in unison, provided that waves start at the same instant; the intensity of the sound being increased by re-enforcement. The differences between the 1st and 8th, the 1st and 5th, the 1st and 3d, and other harmonious combinations, is so great that there are no beats and no discord, the more rapid waves re-enforcing the harmonics of the primary sound. It is important to remember in this connection, that resultant tones are equal to the difference in the rates of vibration of two harmonious tones. Taking a note of 240 vibrations, and its 5th, with 360 vibrations, these two have a difference of 120, which is the lower octave of the 1st and is an harmonious tone.

It is evident that the laws just stated are applicable to overtones, resultant tones and additional tones, which, like the primary notes, have their beats and dissonances.

*Tones by Influence.*—After what has been stated in regard to the laws of musical vibrations, it will be easy to comprehend the production of sounds by influence. If a key of the piano be lightly touched, so as to raise the damper but not to sound the string, and then a note be sung in unison, the string will return the sound, by the influence of the sound-waves of the voice. The sound thus produced by the string will have its fundamental tone and overtones; but the series of overtones will be complete, for none of the nodes are abolished, as in striking or plucking a string at any particular point. If instead of a note in unison, any of the octaves be sounded, the string will return the exact note sung; and the same is true of the 3d, 5th etc. If a chord in harmony with the undamped string be struck, this chord will be exactly returned by influence. In other words, a string may be made to sound by influence, its fundamental tone, its harmonics and harmonious combinations. To carry the observation still farther, the string will return, not only a note of its exact pitch and its harmonics, but notes of the peculiar quality of the primary note. This is a very important point in its applications to the physiology of hearing and can be readily illustrated. Taking identical notes in succession, produced by the voice, trumpet, violin, clarinet or any other musical instrument, it can easily be noted that the quality of the note, as well as the pitch, is rendered by a resounding string; and the same is true of combinations of notes. These laws of tones by influence have been illustrated by strings merely for the sake of simplicity; but they have a more or less perfect application to all bodies capable of producing musical tones, except that some are thrown into vibration with more difficulty than others.

A thin membrane, like a piece of bladder or thin rubber, stretched over a circular orifice, such as the mouth of a wide bottle, may readily be tuned to a certain note. When arranged in this way, the membrane can be made to sound its fundamental note by influence. In addition, the membrane, like a string, will divide itself so as to sound the harmonics of the fundamental, and it will likewise be thrown into vibration by the 5th, 3d etc., of its fundamental, thus obeying the laws of vibrations of strings, although the harmonic sounds are produced with greater difficulty.

The account just given of some of the laws of sonorous vibrations and their relations to musical effects and combinations, although by no means complete, may seem rather extended for a work on physiology; but it should be borne in mind that the mechanism of the appreciation of musical sounds includes the entire physiology of audition. This subject can not be comprehended without a general knowledge of the physics of sound and of some of the laws of harmony; for not only is there a perception of single notes by the auditory apparatus, but the most intricate combinations of sounds in harmony are all appreciated together and at one and the same instant, as will be seen in studying the action and uses of different parts concerned in audition. Many of the laws of musical combinations are directly applicable to the physiology of hearing.

## Uses of Different Parts of the Auditory Apparatus.

The uses of the pavilion and of the external auditory meatus are sufficiently apparent. The pavilion serves to collect the waves of sound, and probably it inclines them toward the external meatus as they come from various directions. Although this action is simple, it has a certain degree of importance, and the various curves of the concavity of the pavilion tend more or less to concentrate sonorous vibrations. Such has long been the opinion of physiologists, and this seems to be carried out by experiments in which the concavities of the external ear have been obliterated by wax. There probably is no resonance or vibration of much importance until the waves of sound strike the membrana tympani. The same remarks may be made with regard to the external auditory meatus. It is not known precisely how the obliquity and the curves of this canal affect the waves of sound, but it is probable that the deviation from a straight course protects, to a certain extent, the tympanic membrane from impressions that might otherwise be too violent.

*Structure of the Membrana Tympani.*—The general arrangement of the membrana tympani has already been described in connection with the topographical anatomy of the auditory apparatus. The membrane is elastic, about the thickness of ordinary gold-beater's skin, and is subject to various degrees of tension by the action of the muscles of the middle ear and under different conditions of atmospheric pressure within and without the tympanic cavity. Its form is nearly circular; and it has a diameter in the adult, according to Sappey, of a little more than $\frac{3}{8}$ of an inch (10 to 11 mm.) vertically and about $\frac{3}{8}$ of an inch (10 mm.) antero-posteriorly. The excess of the vertical over the horizontal diameter is about $\frac{1}{50}$ of an inch (0·5 mm.)

FIG. 268.—*Right membrana tympani, seen from within.* From a photograph, and somewhat reduced (Rüdinger).

1, head of the malleus, divided; 2, neck of the malleus; 3, handle of the malleus, with the tendon of the tensor tympani muscle; 4, divided tendon of the tensor tympani; 5, 6, portion of the malleus between the layers of the membrana tympani; 7, outer (radiating) and inner (circular) fibres of the membrana tympani; 8, fibrous ring of the membrana tympani; 9, 14, 15, dentated fibres, discovered by Gruber; 10, posterior pocket; 11, connection of the posterior pocket with the malleus; 12, anterior pocket; 13, chorda tympani nerve.

The periphery of the tympanic membrane is received into a little ring of bone, which may be separated by maceration in early life, but which is consolidated with the adjacent bony structures in the adult. This bony ring is incomplete at its superior portion, but aside from this, it resembles the groove which receives the crystal of a watch. At the periphery of the membrane, is a ring of condensed, fibrous tissue, which is received into the bony ring. This ring also presents a break at its superior portion.

The concavity of the membrana tympani presents outward, and it may be increased or diminished by the action of the muscles of the middle ear. The point of greatest concavity, where the extremity of the handle of the malleus is attached, is called the umbo. Upon the inner surface of the membrane are two pouches, or pockets. One is formed by a small, irregular, triangular fold, situated at the upper part of its posterior half and consisting of a process of the fibrous layer. This, which is called the posterior pocket, is open below and extends from the posterior upper border of the membrane, to the handle of the malleus, which it assists in holding in position. "After it has been divided, the bone is much more movable than before" (Tröltsch). The anterior pocket is lower and shorter than the posterior. It is formed by a small, bony process turned toward the neck of the malleus, by the mucous membrane, by the bony process of the malleus, by its anterior ligament, the chorda tympani and the anterior tympanic artery. The handle of the malleus is inserted between the two layers of the fibrous structure of the membrana tympani and occupies the upper half of its vertical diameter, extending from the periphery to the umbo.

The membrana tympani, though thin and translucent, presents three distinct layers. Its outer layer is a very thin extension of the integument lining the external meatus, presenting, however, neither papillæ nor glands. The inner layer is a delicate continuation of the mucous membrane lining the tympanic cavity and is covered by tessellated epithelial cells. The fibrous portion, or lamina propria, is formed of two layers. The outer layer consists of fibres radiating from the handle of the malleus to the periphery. These are best seen near the centre. The inner layer is composed of circular fibres, which are most abundant near the periphery and diminish in number toward the centre.

The color of the membrana tympani, when it is examined with an aural speculum by daylight, is peculiar, and it is rather difficult to describe, as it varies in the normal ear in different individuals. Politzer described the membrane, examined in this way, as translucent, and of a color which "most nearly approaches a neutral gray, mingled with a weaker tint of violet and light yellowish-brown." This color is modified, in certain portions of the membrane, by the chorda tympani and the bones of the ear, which produce some opacity. The entire membrane in health has a soft lustre. In addition there is seen, with proper illumination, a well-marked, triangular cone of light, with its apex at the end of the handle of the malleus, spreading out in a downward and forward direction, and $\frac{1}{16}$ to $\frac{1}{12}$ of an inch (1·6 to 2·1 mm.) broad at its base. This appearance is regarded by physiologists as very important, as indicating a normal condition of the membrane. It is undoubtedly due to reflection of light and not to a peculiar structure of that portion of the membrane upon which it is seen.

*Uses of the Membrana Tympani.*—It is unquestionable that the membrana tympani is very important in audition. In cases of disease in which the membrane is thickened, perforated or destroyed, the acuteness of hearing is always more or less affected. That this is in great part due to the absence of a vibrating surface for the reception of waves of sound, is shown by the relief which is experienced by those patients who can tolerate the presence of an artificial membrane of rubber. As regards the mere acuteness of hearing, aside from the pitch of sounds, the explanation of the action of the membrane is very simple. Sonorous vibrations are not readily transmitted through the atmosphere to solid bodies, like the bones of the ear; and when they are thus transmitted they lose considerably in intensity. When, however, the aërial vibrations are received by a membrane, under the conditions of the membrana tympani, they are transmitted with very little loss of intensity; and if this membrane be connected with solid bodies, like the bones of the middle ear, the vibrations are readily conveyed to the sensory portions of the auditory apparatus. The parts composing the middle ear are well adapted to the transmission of sonorous waves to the auditory nerves. The membrane of the tympanum is delicate in structure, stretched to the proper degree of tension, and vibrates under the influence of the waves of sound. Attached to this membrane, is the angular chain of bones, which conducts its vibrations, like the bridge of a violin, to the liquid of the labyrinth. The membrane is fixed at its periphery and has air upon both sides, so that it is under favorable conditions for vibration.

A study of the mechanism of the ossicles and muscles of the middle ear shows that the membrana tympani is subject to certain physiological variations in tension, due to the contraction of the tensor tympani. It is also evident that this membrane may be drawn in and rendered tense by exhausting or rarefying the air in the drum. If the mouth and nose be closed and an attempt be made to breathe forcibly by expanding the chest, the external pressure tightens the membrane. In this condition the ear is rendered insensible to grave sounds, but high-pitched sounds appear to be more intense. If the tension be removed, as may be done by an act of swallowing, the grave sounds are heard with normal distinctness. This experiment, tried at a concert, produces the curious effect of abolishing a great number of the lowest tones, while the shrill sounds are heard very acutely. The same phenomena are observed when the external pressure is increased by descent in a diving-bell.

Undoubted cases of voluntary contraction of the tensor tympani have been observed by otologists; and in these, by bringing this muscle into action, the limit of the perception of high tones is greatly increased. In two instances of this kind, recorded by Blake, the ordinary limit of perception was found to be three thousand single vibrations, and by contraction of the muscle, this was increased to five thousand single vibrations.

The concave form of the membrana tympani and the presence of a bony process between its layers, which is part of the chain of bones of the middle ear, are conditions under which it is impossible that it should have a single, fundamental tone. This has been shown by experiments with stretched membranes depressed in their central portion by means of a solid rod. No membrane can have a single, fundamental tone unless it be in a condition of uniform tension, like a string, and this is impossible in the membrana tympani. Nevertheless the membrana tympani repeats sounds by influence, and it is capable of repeating in this way a much greater variety of sounds than if it had itself a fundamental tone and were capable of a uniform degree of tension. This has been shown by experiments with stretched, elastic membranes made to assume a concave form. If the membrana tympani had a single, fundamental tone, it would vibrate by influence only with certain tones in unison with it, and the overtones would be eliminated. It would then act like a resonator closed by a membrane, and the tone with which it happened to be in unison would overpower all other tones. The fact is that all tones, the vibrations of which reach the membrane, are appreciated at their proper value as regards intensity. Again, if the membrana tympani had its own fundamental tone, it would have overtones of the fundamental, which would produce errors and confusion in auditory appreciation. The chain of bones, also, attached to the membrane, acts as a damper and prevents the persistence of vibrations after the waves of sound cease in the air. This provision enables rapid successions of sounds to be distinctly and acurately repeated.

The arrangement of the muscles and bones of the middle ear is such that the tension of the membrana tympani may be regulated and graduated with great nicety. It does not seem to be necessary to perfect audition that this should be done for every single note or combination of notes, but the membrane probably is brought by voluntary effort to a definite degree of tension for notes within a certain range as regards pitch or for successions and progressions of sounds in a particular key. As far as the consciousness of this muscular action is concerned, it may be revealed only by the fact of the correct appreciation of certain musical sounds. Some persons can educate the ear so as to acquire what is called the faculty of absolute pitch; that is, without the aid of a tuning-fork or any musical instrument, they can give the exact musical value of any given note. A possible explanation of this is that such persons may have educated the muscles of the ear so as to put the tympanic membrane in such a condition of tension as to respond to a given note and to recognize the position of this note in the musical scale. Finally, an accomplished musician, in conducting an orchestra, can by a voluntary effort, direct his attention to certain instruments and hear their notes distinctly, separating them from the general volume of sound, can distinguish the faintest discords and can designate a single instrument making a false note.

Destruction of both tympanic membranes does not necessarily produce total deafness, although this condition involves considerable impairment of hearing. So long as there is simple destruction of these membranes, the bones of the middle ear and the other parts of the auditory apparatus being intact, the waves of sound are conducted to the auditory nerves, although this is done imperfectly. In a case reported by Astley Cooper, one membrana tympani was entirely destroyed, and the other was nearly gone, there being some parts of its periphery remaining. In this person the hearing was somewhat impaired, although he could distinguish ordinary conversation without much difficulty. Fortunately he had considerable musical taste, and it was ascertained that his musical ear was not seriously impaired; "for he played well on the flute and had frequently borne a part in a concert. I speak this, not from his authority only, but also from that of his father, who is an excellent judge of music, and plays well on the violin: he told me, that his son, besides playing on the flute, sung with much taste, and perfectly in tune."

There is an important consideration that must be kept in view in studying the uses of any distinct portion of the auditory apparatus, like the membrana tympani. This membrane, like all other parts of the apparatus, except the auditory nerves themselves, has simply an accessory action. If the regular waves of a musical sound be conveyed to the terminal filaments of the auditory nerves, these waves make their impression and the sound is correctly appreciated. It makes no difference, except as regards intensity, how these waves are conducted; the sound is appreciated by the impression made upon the nerves, and the nerves only. The waves of sound are not like the waves of light, refracted, decomposed, perhaps, and necessarily brought to a focus as they impinge upon the retina; but as far as the action of the accessory parts of the ear are concerned, the waves of sound are unaltered; that is, the rate of their succession remains absolutely the same, though they be reflected by the concavities of the concha and repeated by the tympanic membrane. Even if it be assumed that the membrane under normal conditions repeats musical sounds by vibrations produced by influence, and that sounds are exactly repeated, the position of these sounds in the musical scale is not and can not be altered by the action of any of the accessory organs of hearing. The fact that a person may retain his musical ear with both membranes destroyed is not really an argument against the view that the membrane repeats sounds by influence; for if musical sounds or noisy vibrations be conducted to the auditory nerves, the impression produced must of necessity be dependent exclusively upon the character, regularity and number of the sonorous vibrations. And, again, the physical laws of sound teach that a membrane, like the membrana tympani, must reproduce sounds with which it is more or less in unison much more perfectly than discordant or irregular vibrations. In a loud confusion of noisy sounds, one can readily distinguish melody or harmony, even when the vibrations of the latter are comparatively feeble.

It has been shown that the appreciation of the pitch of sounds bears a certain relation to the degree of tension of the tympanic membrane. When the membrane is rendered tense, there is insensibility to low notes. When the membrane is brought to the highest degree of tension by voluntary contraction of the tensor tympani, the limit of appreciation of high notes may be raised from three thousand to five thousand vibrations. It is a fact in the physics of the membrana tympani that the vibrations are more intense the nearer the membrane approaches to a vertical position; and it has been observed that the membrane has a position more nearly vertical in musicians than in persons with an imperfect musical ear (Tröltsch).

Experiments have shown that the tympanic membrane vibrates more forcibly when relaxed than when it is tense. In certain cases of facial palsy, in which it is probable that the branch of the facial going to the tensor tympani was affected, the ear has been found painfully sensitive to powerful impressions of sound. This probably has no relation to pitch, and most sounds that are painfully loud are comparatively grave. Artillerists are in danger of rupture of the membrana tympani from sudden concussions. To guard against this injury, it is recommended to stop the ear, draw the shoulder up against the ear most in danger, and particularly to inflate the middle ear after Valsalva's method. "This method consists in making a powerful expiration, with the mouth and nostrils closed" (Tröltsch).

*Mechanism of the Ossicles of the Ear.*—The ossicles of the middle ear, in connection with the muscles, have a twofold office: First, by the action of the muscles the membrana tympani may be brought to different degrees of tension. Second, the angular chain of bones serves to conduct sonorous vibrations to the labyrinth. It must be remembered that the handle of the malleus is closely attached to the membrana tympani, especially near its lower end. Near the short process—which is a little, conical projection at the root of the handle—the attachment is looser and there is even an incomplete joint-space at this point. The long process is attached closely to the Glasserian fissure of the temporal bone.

The malleus is articulated with the incus by a very peculiar joint. This joint is so arranged, presenting a sort of cog, that the handle of the malleus can rotate only outward; and when a force is applied which would have a tendency to produce a rotation inward, the malleus must carry the incus with it. This mechanism has been compared to that of a watch-key with cogs which are fitted together and allow the whole key to turn in one direction, but are separated so that only the upper portion of the key turns when the force is applied in the opposite direction (Helmholtz). In the articulation between the malleus and the incus, the only difference is that there is but one cog; but this is sufficient to prevent an independent rotation of the malleus inward.

The body of the incus is attached to the posterior bony wall of the tympanic cavity. Its articulation with the malleus has just been indicated. By the extremity of its long process, it is also articulated with the stapes, which completes the chain. *In situ*, the stapes forms nearly a right angle with the long process of the incus.

The stapes is articulated with the incus, as indicated above, and its oval base is applied to the fenestra ovalis. Surrounding the base of the stapes, is a ring of elastic fibro-cartilage, which is closely united to the bony wall of the labyrinth, by an extension of the periosteum.

The articulations between the malleus and the incus and between the incus and the stapes are so arranged that when the membrana tympani is forced outward, as it may be by inflation of the tympanic cavity, there is no danger of tearing the stapes from its attachment to the fenestra ovalis; for when the handle of the malleus is drawn outward, the cog-joint between the malleus and the incus is loosened and no considerable traction can be exerted upon the stapes.

The tensor tympani is by far the more important of the two muscles of the middle ear. Its action is to tighten the cog-like joint between the malleus and the incus, to tighten, also, all the ligaments of the incus, to draw the long process of the malleus inward, thereby increasing the tension of the membrana tympani, and to press the base of the stapes against the fenestra ovalis. By the action of this muscle the chain of ossicles becomes practically a solid and continuous, angular, bony rod.

Although experiments have demonstrated the mechanism of the ossicles and the action of the tensor tympani, both as regards the chain of bones and the membrana tympani, direct observations are wanting, to show the exact relations of these different conditions of the ossicles and of the membrane to the physiology of audition. One very important physical point, however, which has been the subject of much discussion, is settled. The chain of bones acts as a single, solid body in conducting vibrations to the labyrinth. It is a matter of physical demonstration that vibrations of the bones themselves would be infinitely rapid as compared with the highest tones which can be appreciated by the ear, if it were possible to induce in these bones regular vibrations. Practically, then, the ossicles have no independent vibrations that can be appreciated. This being the fact, the ossicles simply conduct to the labyrinth the vibrations induced in the membrana tympani by sound-waves; and their arrangement is such that these vibrations lose very little in intensity. While it has been shown experimentally that the amplitude of vibration in the membrana tympani and the ossicles diminishes as the tension of the membrane is increased, it would seem that when the tensor tympani contracts, it must render the conduction of sound-waves to the labyrinth more delicate than when the auditory apparatus is in a relaxed condition, which may be compared with the "indolent" condition of accommodation of the eye. When the membrana tympani is relaxed and the cog-like articulation between the malleus and the incus is loosened, the vibrations of the membrane and of the malleus may have a greater amplitude; but when the malleo-incudal joint is tightened and the stapes is pressed against the fenestra ovalis, the loss of intensity of vibration, in conduction through the bones to the labyrinth, must be reduced to the minimum. With this view, the tensor tympani muscle, while it contracts to secure for the membrana tympani the degree of tension most favorable for vibration under the influence of certain sounds, puts the chain of bones in the condition best adapted to the conduction of the vibrations of the membrane to the labyrinth, with the smallest possible loss of intensity.

## Physiological Anatomy of the Internal Ear.

The internal ear consists of the labyrinth, which is divided into the vestibule, semicircular canals and cochlea. The general arrangement of these parts has already been described; and it remains only to study the structures contained within the bony labyrinth, in so far as their anatomy bears directly upon the physiology of audition. Passing inward from the tympanum, the first division of the internal ear is the vestibule. This cavity communicates with the tympanum, by the fenestra ovalis, which is closed in the natural state by the base of the stapes. It communicates, also, with the semicircular canals and with the cochlea.

*General Arrangement of the Membranous Labyrinth*—The bony labyrinth is lined by a moderately thick periosteum, consisting of connective tissue, a few delicate, elastic fibres, nuclei and blood-vessels, with spots of calcareous concretions. This membrane adheres closely to the bone and extends over the fenestra ovalis and the fenestra rotunda. Its inner surface is smooth and is covered with a single layer of cells of endothelium, which in some parts is segmented and in others forms a continuous, nucleated sheet. In certain portions of the vestibule and semicircular canals, the periosteum is united to the membranous labyrinth, more or less closely, by fibrous bands, which have been called ligaments of the labyrinth. The fenestra rotunda, which lies between the cavity of the tympanum and the cochlea, is closed by a membrane formed by an extension of the periosteum lining the cochlea, on one side, and the mucous membrane lining the tympanic cavity, on the other.

In the bony vestibule, occupying about two-thirds of its cavity, are two distinct sacs; a large, ovoid sac, the utricle, situated in the upper and posterior portion of the cavity, and a smaller, rounded sac, the saccule, situated in its lower and anterior portion. These two sacs communicate with each other through a small canal in the form of the letter Y, which is represented in the upper diagram in Fig. 269. The utricle communicates with the semicircular canals, and the saccule opens into the membranous canal of the cochlea, by the canalis reuniens. At a point in the utricle corresponding to the entrance of a branch of the auditory nerve, is a round, whitish spot, called the acoustic spot (macula acustica), containing otoliths, or otoconia, which are attached to the inner surface of the membrane. A similar spot, containing otoliths, exists in the saccule, at the point of entrance of its nerve. Otoliths are also found in the ampullæ of the semicircular canals. These calcareous masses are composed of crystals of calcium carbonate, which are hexagonal and pointed at their extremities. Nothing definite is known of the uses of these calcareous bodies, which exist in man, mammals, birds and reptiles.

FIG. 269.—*Diagram of the labyrinth (vestibule and semicircular canals).* From a photograph, and somewhat reduced (Rüdinger).

Upper figure: 1, utricle; 2, saccule; 3, 5, membranous cochlea; 4, canalis reuniens; 6, semicircular canals.

Lower figure: 1, utricle; 2, saccule; 3, 4, 6, ampullæ; 5, 7, 8, 9, semicircular canals; 10, auditory nerve (partly diagrammatic); 11, 12, 13, 14, 15, distribution of the branches of the nerve, to the vestibule and the semicircular canals.

The membranous semicircular canals occupy about one-third of the cavity of the bony canals. They present small, ovoid dilatations, called ampullæ, corresponding to the ampullary enlargements of the bony canals. They are held in place by a large number of little, fibrous bands extending to the bony labyrinth.

The membrane of the cochlea, including the lining periosteum, occupies the spiral canal of the cochlea, which it fills completely. Viewed externally, it appears as a single tube, following the turns of the bony cochlea, beginning below, at the first turn, by a blind extremity, and terminating in a blind extremity at the summit of the cochlea. If a section of the cochlea be made in a direction vertical to the spiral, it will be seen that this canal is divided, partly by bone and partly by membrane, into an inferior portion, a superior portion, and a triangular canal, lying between the two, which is external. The bony septum is in the form of a spiral plate, extending from the central column (the modiolus) into the cavity of the cochlea, about half-way to its external wall, and terminating above in a hook-shaped extremity, called the hamulus. The free edge of this bony lamina is thin and dense. Near the central column it divides into two plates, with an intermediate, spongy structure, in which are lodged vessels and nerves. The surface of the bony lamina looking toward the base of the cochlea is marked by a number of regular, transverse ridges, or striæ.

FIG. 270.—*Otoliths from various animals* (Rüdinger).
1, from the goat; 2, from the herring; 3, from the devil-fish; 4 from the mackerel; 5, from the flying-fish; 6, from the pike; 7, from the carp; 8, from the ray; 9, from the shark; 10, from the grouse.

Attached to the free margin of the bony lamina, is a membrane, the membrana basilaris, which extends to the outer wall of the cochlea. In this way the canal of the cochlea is divided into two portions, one above and the other below the septum. The portion below begins at the fenestra rotunda and is called the scala tympani. The portion above, exclusive of the triangular canal of the cochlea, communicates with the vestibule and is called the scala vestibuli.

Above the membrana basilaris, is a membrane, the limbus laminæ spiralis, the external continuation of which is called the membrana tectoria, or the membrane of Corti. Between the membrana tectoria and the membrana basilaris, is the organ of Corti. The membrane of Reissner extends from the inner portion of the limbus upward and outward to the outer wall of the cochlea. This divides the portion of the cochlea situated above the scala tympani into two portions; an internal portion, the scala vestibuli, and an external, triangular canal, called the canalis cochleæ, or the membranous cochlea.

In the anatomical description of the contents of the bony cochlea, the membranous parts may be designated as follows:

1. The portion below the bony and membranous septum, called the scala tympani. This is formed by the periosteum lining the corresponding portion of the cochlea and the under surface of the bony lamina, and the membrana basilaris.

2. The scali vestibuli. This is formed by the periosteum lining the cor-

FIG. 271.—*Section of the first turn of the spiral canal of a cat newly-born.—Section of the cochlea of a human fœtus at the fourth month.* From a photograph, and somewhat reduced (Rüdinger).

Upper figure: 1, 2, 6, lamina spiralis; 2, lower plate; 3, 4, 5, 5, nervus cochlearis; 7, membrane of Reissner; 8, membrana tectoria; 9, epithelium; 10, 11, pillars of Corti; 12, inner hair-cells; 13, outer hair-cells; 14, 16, membrana basilaris; 15, epithelium in the sulcus spiralis; 17, 18, 19, ligamentum spirale; 20, spiral canal, below the membrana basilaris.

Lower figure: S T, S T, 5, 5, 7, 7, 8, 8, scala tympani; S V, S V, 9, 9, scala vestibuli; 1, base of the cochlea; 2, apex; 3, 4, central column; 10, 10, 10, 10, ductus cochlearis; 11, branches of the nervus cochlearis; 12, 12, 12, spiral ganglion; 13, 14, limbus laminæ spiralis; 15, membrane of Reissner; 16, epithelium; 17, outer hair-cells; 18, epithelium of the membrana basilaris; 19, nervous filaments; 20, union of the membrana basilaris with the ligamentum spirale; 21, epithelium of the peripheral wall of the ductus cochlearis; 22, 23, membrana tectoria; 24, spiral canal, below the membrana basilaris.

responding portion of the bony cochlea and the upper surface of the bony septum and is bounded externally by the membrane of Reissner.

3. The true membranous cochlea. This is the spiral, triangular canal,

bounded externally by the periosteum of the corresponding portion of the wall of the cochlea, internally, by the membrane of Reissner, and on the other side, by the membrana basilaris. What is thus called the membranous cochlea is divided by the limbus laminæ spiralis and the membrana tectória into two portions; a triangular canal above, which is the larger, and a quadrilateral canal below, between the limbus and membrana tectoria and the membrana basilaris. The quadrilateral canal contains the organ of Corti and various complex, anatomical structures. The relations of these divisions of the cochlea are shown in Fig. 272.

The membranous cochlea, as described above, follows the spiral course of the cochlea, terminates superiorly in a blind, pointed extremity, at the cupola, beyond the hamulus, and is connected below with the saccule of the vestibule, by the canalis reuniens. The relations of the different portions of the membranous cochlea to each other and to the scalæ of the cochlea are shown in Fig. 271.

*Liquids of the Labyrinth.*—The labyrinth contains a certain quantity of a clear, watery liquid, called the humor of Cotugno or of Valsalva. A portion of this liquid surrounds the membranous sacs of the vestibule, the semicircular canals and the membranous cochlea, and this is known as the perilymph of Breschet. Another portion of the liquid fills the membranous labyrinth; and this is sometimes called the humor of Scarpa, but it is known more generally as the endolymph of Breschet. The perilymph occupies about one-third of the cavity of the bony vestibule and semicircular canals and both scalæ of the cochlea. Both this liquid and the endolymph are clear and watery, becoming somewhat opalescent on the addition of alcohol. The spaces in the labyrinth are directly connected with the lymphatic system. The space occupied by the perilymph communicates with lymphatics, chiefly through the aqueduct of the cochlea, but there is also a communication through the internal auditory meatus, with the space beneath the dura mater. The endolymph passes to the subarachnoid space, beneath the arachnoid covering of the auditory nerve. As far as is known, the uses of the liquid of the internal ear are to sustain the delicate structures contained in this portion of the auditory apparatus and to conduct sonorous vibrations to the terminal filaments of the auditory nerves and the parts with which they are connected.

*Distribution of the Nerves in the Labyrinth.*—As the auditory nerves enter the internal auditory meatus, they divide into an anterior, or cochlear, and a posterior, or vestibular branch. The vestibular branch divides into three smaller branches, a superior and anterior, a middle, and a posterior branch. The superior and anterior branch, the largest of the three, is distributed to the utricle, the superior semicircular canal and the external semicircular canal. The middle branch is distributed to the saccule. The posterior branch passes to the posterior semicircular canal. The nerves distributed to the utricle and saccule penetrate at the points occupied by the otoliths, and the nerves going to the semicircular canals pass to the ampullæ, which also contain otoliths. (See Fig. 269.) In each ampulla, at the point where the nerve enters, is a transverse fold, projecting into the canal and occupying about one-third of its circumference, called the septum transversum.

The nerves terminate in essentially the same way in the sacs of the vestibule and the ampullæ of the semicircular canals. At the points where the nerves enter, in addition to the otoliths, are cylindrical cells of various forms, which pass gradually into the general endothelium of the cavities. In addition to these cells, are fusiform, nucleated bodies, the free ends of which are provided with hair-like processes, called fila acustica. These are about $\frac{1}{800}$ of an inch (31 $\mu$) in length and are distributed in quite a regular manner around the otoliths. The nerves form an anastomosing plexus beneath the endothelium, and they probably terminate in the fusiform bodies just described as presenting the fila acustica at their free extremities. In the sacs of the vestibule and in the semicircular canals, nerves exist only in the macula acustica and the ampullæ.

The cochlear division of the auditory nerve breaks up into a number of small branches, which pass through foramina at the base of the cochlear, in what is called the tractus spiralis foraminulentus. These follow the axis of the cochlea and pass in their course toward the apex, between the plates of the bony spiral lamina. Between these plates of bone, the dark-bordered nerve-fibres pass each one through a bipolar cell, these cells together forming a spiral ganglion, known as the ganglion of Corti. Beyond this ganglion the nerves form an anastomosing plexus and finally enter the quadrilateral canal, or the canal of Corti. As they pass into this canal they suddenly become pale and exceedingly fine. They probably are connected finally with the organ of Corti, although their exact mode of termination has not yet been determined. The course of the nerve-fibres to their distribution in the cochlea is shown in Fig. 272.

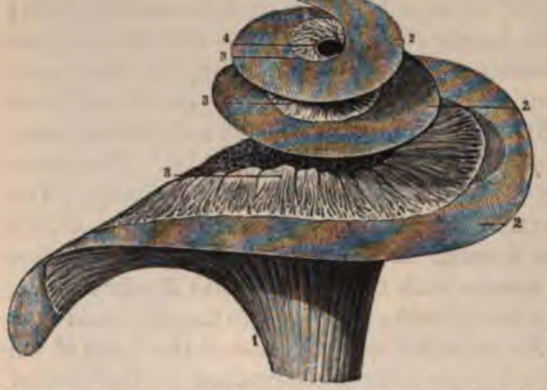

FIG. 272.—*Distribution of the cochlear nerve in the spiral lamina of the cochlea. The cochlea is from the right side and is seen from its antero-inferior part* (Sappey).

1, trunk of the cochlear nerve; 2, 2, 2, membranous zone of the spiral lamina: 3, 3, 3, terminal expansion of the cochlear nerve, exposed in its whole extent by the removal of the superior plate of the lamina spiralis: 4, orifice of communication of the scala tympani with the scala vestibuli.

*Organ of Corti.*—In the quadrilateral canal, bathed in the endolymph, throughout its entire, spiral course, is an arrangement of pillars, or rods, which are regular, like the strings of a harp in miniature. These are the pillars of Corti. These pillars are external and internal, with their bases attached to the basilar membrane and their summits articulated above, so as to form a regular, spiral arcade, enclosing a triangular space which is bounded below by the basilar membrane. The number of the elements of the organ of Corti is estimated at about 4,500, for the outer, and 6,500, for the inner rods. The relations of these structures to the membranous labyrinth are seen in Fig. 271. The external pillars are longer, more delicate and more rounded than


FIG. 273.—*The two pillars of the organ of Corti* (Sappey).

A, external pillar of the organ of Corti: 1, body, or middle portion; 2, posterior extremity, or base; 3, cell on its internal side; 4, anterior extremity; 5, convex surface, by which it is joined to the internal pillar; 6, prolongation of this extremity.
B, internal pillar of the organ of Corti: 1, body, or middle portion; 2, posterior extremity; 3, cell on its external side; 4, anterior extremity; 5, concave surface, by which it is joined to the external pillar; 6, prolongation, lying above the corresponding prolongation of the external pillar.
C, the two pillars of the organ of Corti, united by their anterior extremity, and forming an arcade, the concavity of which presents outward: 1, 1, body, or middle portion of the pillars; 2, 2, posterior extremities; 3, 3, cells attached to the posterior extremities; 4, 4, anterior extremities joined together; 5, terminal prolongation of this extremity.

the internal pillars. The form of the pillars is more exactly shown in Figs. 273 and 274, the latter figure, however, exhibiting other structures which enter into the constitution of the organ of Corti. It will be remarked that


FIG. 274.—*Vertical section of the organ of Corti of the dog; magnified 800 diameters* (Waldeyer).

*a–b*, homogeneous layer of the basilar membrane; *v*, tympanic layer, with nuclei, granular cell-protoplasm and connective tissue; $a_1$, tympanic lip of the crista spiralis; *c*, thickened portion of the basilar membrane; *d*, spiral vessel; *e*, blood-vessel; *f*, *h*, bundle of nerves; *g*, epithelium; *i*, inner hair-cell, with its basilar process, *k*; *l*, head-plate of the inner pillar; *m*, union of the two pillars; *n*, base of the inner pillar; *o*, base of the outer pillar; *p*, *q*, *r*, outer hair-cells, with traces of the cilia; *t*, bases of two other hair-cells; *z*, Hensen's prop-cell; $l$–$l_1$, lamina reticularis; *w*, nerve-fibre passing to the first hair-cell, *p*.

a small, nucleated body is attached to the base of each pillar. At the summit, where the internal and the external pillars are joined together, is a delicate prolongation, directed outward, which is attached to the covering of the quadrilateral canal.

The above description comprises about all that is definitely known of the arrangement of the pillars, or rods of Corti. They are nearly homogeneous, except when treated with reagents, and are said to be of about the consistence of cartilage. They are closely set together, with very narrow spaces between them, and it is difficult to see how they can be stretched to any considerable degree of tension. The arch is longer at the summit than at the base of the cochlea, the longest rods, at the summit, measuring, according to Pritchard, about $\frac{1}{200}$ of an inch (125 $\mu$), and the shortest, at the base, about $\frac{1}{500}$ of an inch (50 $\mu$). At the base of the cochlea the two sets of rods are about equal in length. From the base to the apex, both sets, outer and inner, progressively increase in length, and the outer rods become the longer, so that near the apex they are nearly twice as long as the inner. The anatomical relations between the pillars and the terminal filaments of the auditory nerves are not definitely settled.

In addition to the pillars just described, various cellular elements enter into the structure of the organ of Corti. The most important of these are the inner and the outer hair-cells. These are 16,400 to 20,000 in number (Hensen, Waldeyer). The inner hair-cells are arranged in a single row, and the outer hair-cells, in three rows. Nothing definite is known of the uses of these cells. The relations of these parts are shown in Fig. 274. It is supposed by some anatomists that the filaments of the auditory nerves terminate in the cells above described; but this point is not definitely settled.

## Uses of Different Parts of the Internal Ear.

The precise uses of the different parts found in the internal ear are obscure, notwithstanding the careful researches that have been made into the anatomy and the physiology of the labyrinth. There are several points, however, bearing upon the physiology of this portion of the auditory apparatus, concerning which there can be no doubt:

First, it is certain that impressions of sound are received by the terminal filaments of the auditory nerves and by these nerves are conveyed to the brain.

Second, the uses of the parts composing the external and the middle ear are chiefly accessory. The sonorous waves are collected by the pavilion and are conveyed by the external meatus, to the middle ear; the membrana tympani vibrates under their influence; and they are thus collected, repeated and transmitted to the internal ear.

*Uses of the Semicircular Canals.*—In the experiments of Flourens, upon pigeons and rabbits (1824), it was shown that destruction of the semicircular canals had apparently no effect upon the sense of hearing, while destruction of the cochlea upon both sides produced complete deafness. In addition it was observed that destruction of the semicircular canals on both sides was followed by remarkable disturbances in equilibration. The animals could maintain the standing position, but so soon as they made any movements, "the head began to be agitated; and this agitation increasing with the movements of the body, walking and all regular movements finally became impossible, in nearly the same way as when equilibrium and stability of movements are lost after turning several times or violently shaking the head." These observations of Flourens, at least as far as regards the influence of the semicircular canals upon equilibration, have been confirmed by Goltz and are sustained by observations upon the human subject in the condition known as Ménierè's disease. As far as can be judged from experimental *data*, it does not seem probable that the nerves directly concerned in audition are distributed to any considerable extent in the semicircular canals. Indeed the uses of these parts is exceedingly obscure; for it can hardly be admitted, upon purely anatomical grounds, that they are concerned in the discrimination of the direction of sonorous vibrations, an idea which has been advanced by some physiologists.

*Uses of the Parts contained in the Cochlea.*—There can be no doubt with regard to the capital point in the physiology of the cochlea; namely, that those branches of the auditory nerve which are essential to the sense of hearing and which receive the impressions of sound are distributed mainly in the cochlea. An analysis of sonorous impressions shows that they possess various attributes, such as intensity, quality and pitch. As far as the terminal filaments of the auditory nerve are concerned, it is evident that the intensity of sound is appreciated in proportion to the power of the impression made upon these nerves. With regard to quality of sound, it has been seen that this is due to the form of sonorous vibrations, and that musical sounds usually are compound, their quality depending largely upon the relative power of the harmonics, partial tones etc. It has also been seen that consonating bodies repeat by influence, not only the actual pitch of tones, but their quality. If there be in the cochlea an anatomical arrangement of rods or fibres by which the sonorous vibrations conveyed to the ear by the atmosphere are repeated, there is reason to believe that the quality as well as the pitch is reproduced.

The arrangement of the rods which enter into the structure of the organ of Corti has afforded a theoretical explanation of the final mechanism of the appreciation of pitch. With the exception of the internal ear, the action of different portions of the auditory apparatus is simply to conduct and repeat sonorous vibrations; and the sole use of these accessory parts, aside from the protection of the organs, is to convey the vibrations to the terminal, nervous filaments. Whatever be the uses of the membrana tympani in repeating sounds by influence, it is certain that this membrane possesses no true, auditory nerves, and that the auditory nerves only are capable of receiving impressions of sound. Thus hearing, and even the appreciation of pitch, is not necessarily lost after destruction of the membrana tympani; and if sonorous vibrations reach the auditory nerves, they will be appreciated and appreciated correctly.

In view of the arrangement of the organ of Corti, with its eleven thousand or more rods of different lengths arranged with a certain degree of regularity, a number more than sufficient to represent all the notes of the musical scale, it is not surprising that they should be regarded as capable of repeating all the notes heard in music. Helmholtz formulated this idea in the theory that sounds conveyed to the cochlea throw into vibration only those elements of the organ of Corti which are tuned, so to speak, in unison with them. According to this hypothesis, the rods of Corti constitute a harp of several thousand strings, played upon, as it were, by the sonorous vibrations. Theories analogous to the one proposed by Helmholtz, but of course lacking the basis of exact anatomical and physical details developed by modern researches and experiments, were advanced by Du Verney (1683) and by Le Cat (1767).

Viewing the question anatomically, it is by no means certain that the rods of Corti are so attached and stretched that they are capable of separate and individual vibrations. It has not been demonstrated that certain of these rods vibrate under the influence of certain notes or that they are tuned in accord with certain notes. Hensen and others have rejected the theory of Helmholtz, basing their opinions mainly upon the anatomical arrangement of the rods of Corti. Hensen assumed it to be a physical impossibility for the different rods to vibrate individually, and he regarded it as improbable that the rods are tuned in accord with different musical notes. Similar objections apply to the theory that different transverse fibres in the membrana basilaris vibrate in accord with particular notes. There is, indeed, no theory which affords an entirely satisfactory explanation of the mechanism of the final appreciation of the pitch of musical sounds.

It is not absolutely necessary that sonorous vibrations should pass to the cochlea through the external ear and parts in the middle ear. Sounds may be conducted to the auditory nerves through the bones of the head or through the Eustachian tube, as is shown by the simple and familiar experiment of placing a tuning-fork in contact with the head or between the teeth, the ears being closed.

The action of the two ears does not seem to be absolutely necessary to the correct appreciation of auditory impressions; but variations in the force of such impressions, made upon either ear, aid in determining the direction of sounds, although errors are often made in this regard.

The estimate of the distance of sounds is made by judging of the intensity, in connection with information obtained through other senses, especially the sense of sight. The power of estimating distance is largely influenced by experience and education.

*Centres for Audition.*—The centres for audition in dogs and monkeys are in the superior temporo-sphenoidal convolution (Ferrier, Munk). In man these centres are in the first (superior) and second temporal convolutions of the temporo-sphenoidal lobe, which are supplied by the fourth branch of the middle cerebral artery. This has been ascertained by pathological observations as well as by experiments on the lower animals. In man the action of these centres is not completely crossed, and destruction of the centre upon one side does not cause complete deafness in either ear. Complete destruction of the centres on both sides, however, produces total deafness. Injury of the first temporal convolution is often followed by the condition known as word-deafness, in which the subject hears the sound of words, but these sounds convey to him no idea. This is the psychical, auditory centre, and it is confined to the first temporal convolution, on the left side (Wernicke). It is analogous to the condition already described under the name of word-blindness, and like the centre for speech, is usually confined to the left side of the cerebrum. It has been suggested by Westphal that this centre may be on the right side of the cerebrum, in left-handed persons.

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# CHAPTER XXIV.

## *ORGANS AND ELEMENTS OF GENERATION.*

General considerations—Female organs of generation—General arrangement of the female organs—The ovaries—Graafian follicles—The parovarium—The uterus—The Fallopian tubes—Structure of the ovum—Discharge of the ovum—Passage of ova into the Fallopian tubes—Puberty and menstruation—Changes in the Graafian follicle after its rupture (corpus luteum)—Male organs of generation—The testicles—Vesiculæ seminales—Prostate—Glands of the urethra—Male elements of generation—Spermatozoids.

GENERATION is one of the most important of the animal functions, and as such usually is treated of quite fully in works upon physiology; but a more or less extended account of this function is also to be found in every complete treatise on anatomy and in most works on obstetrics. While the physiological history of the human organism would not be complete without touching upon generation and development, it does not seem desirable to give a very full description of these processes, in which there would necessarily be a repetition of what is always to be found in works upon other subjects.

The question of so-called spontaneous generation in some of the lower animals was formerly much discussed by physiologists. This, however, is now of purely historical interest. As actual knowledge of facts has accumulated, the limits of what was thought to be spontaneous generation have become more and more restricted; until now it is generally admitted that spontaneous generation does not exist in the history of animals. The entire question, therefore, may be dismissed with this simple statement. There are, however, certain distinct forms of generation; but the only one that has any considerable importance in connection with human physiology is generation of new beings by the union of male and female elements in the fecundation of the ovum, with the development of the fecundated ovum. This is known as sexual generation. The two elements of generation are developed in separate beings, male and female, and these elements are brought together normally in what is known as sexual connection, or copulation.

### FEMALE ORGANS OF GENERATION.

A knowledge of certain points in the anatomy of the female organs of generation is essential to the comprehension of the most important of the processes of reproduction. Following a fruitful intercourse of the sexes, the function of generation, as regards the male, ceases with the comparatively simple process of penetration of the male element through the protective covering of the ovum and its fusion with the female element. The fecundated ovum then passes through certain changes, which are the first processes of its development, forms its attachments to the body of the mother, continues its development, and is nourished and grows, until the fœtus at term is brought into the world. It will not be necessary to describe minutely the anatomy of the external parts, as these are concerned only in sexual intercourse and in parturition; which latter, though a purely physiological process, forms the greatest part of the science of obstetrics, is considered elaborately in treatises on this subject and usually is not treated of to any great extent in works upon physiology.

The female organs of generation are divided anatomically into internal and external. The external organs are the vulva, the adjacent parts and the vagina. The internal organs are the uterus, Fallopian tubes and the ovaries. The ovaries are the true, female organs, in which alone the female element can be produced. The Fallopian tubes and the uterus are accessory in their uses, the female element, the ovum, passing through the Fallopian tubes to the uterus, where it forms the attachments to the body of the mother, which are essential to its nourishment and full development after fecundation.

The vagina has a direction, slightly curved anteriorly, which is nearly coincident with the axis of the outlet, or the inferior strait of the pelvis. Projecting into the vagina, at its upper extremity, is the lower part of the neck of the uterus. The uterus extends from the vagina nearly to the brim of the pelvis. It is situated between the bladder and the rectum, and has an antero-posterior inclination when the bladder is moderately distended, which brings its axis nearly coincident with that of the superior strait of the pelvis. With the body erect, the angle of the uterus with the perpendicular is about forty-five degrees.

The uterus is held in place by ligaments, certain of which are formed of folds of the peritoneum. The anterior ligament is reflected from the anterior surface to the bladder; the posterior ligament extends from the posterior surface to the rectum; the round ligaments extend from the upper angle of the uterus, on either side, between the folds of the broad ligament and through the inguinal canal, to the symphysis pubis; the broad ligaments extend from the sides of the uterus to the walls of the pelvis.

The uterus and the broad ligaments partially divide the pelvis into two portions; and these ligaments, which are formed of a double fold of peritoneum, present a superior, or posterior surface, and an inferior, or anterior surface. The superior, or anterior border of this fold is occupied by the Fallopian tubes, the peritoneum constituting their outer coat. Laterally, at the free extremities of the tubes, the peritoneum ceases, and there is an actual opening of each Fallopian tube into the peritoneal cavity. Attached to the broad ligament and projecting upon its posterior surface, is the ovary, which is connected with the fibrous tissue between the two layers of the ligament and has no proper peritoneal investment, so that it is actually within the peritoneal cavity.

*The Ovaries.*—The ovaries, attached to the broad ligament and projecting from its posterior surface, lie nearly horizontally in the pelvic cavity, on

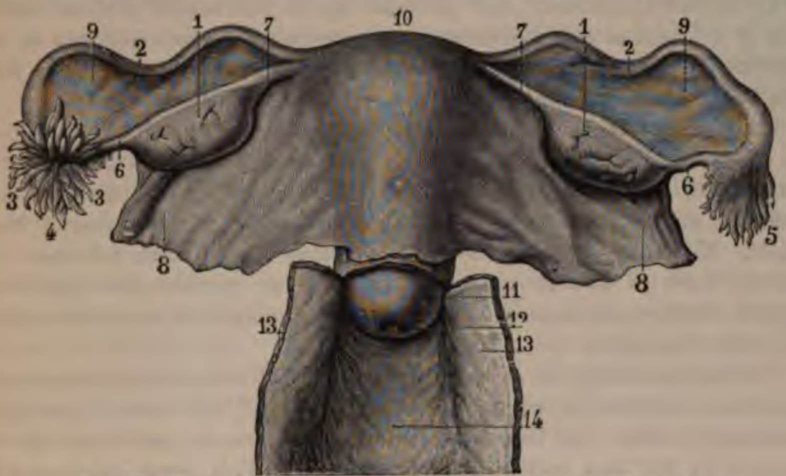


FIG. 275.—*Uterus, Fallopian tubes and ovaries; posterior view* (Sappey).
1, ovaries; 2, 2, Fallopian tubes; 3, 3, fimbriated extremity of the left Fallopian tube, seen from its concavity; 4, opening of the left tube; 5, fimbriated extremity of the right tube, posterior view; 6, 6, fimbriæ which attach the extremity of each tube to the ovary; 7, 7, ligaments of the ovary; 8, 8, 9, 9, broad ligaments; 10, uterus; 11, cervix uteri; 12, os uteri; 13, 13, 14, vagina.

either side of the uterus. They are of a whitish color, and their form is ovoid and flattened, with the anterior border, sometimes called the base, attached to the broad ligament. By closely examining their mode of connection with the broad ligament, it is seen that at the margin of the attached surface of the ovary, the posterior layer of the ligament ceases, and that the fibrous stroma of the medullary portion of the ovary is continuous with the fibrous tissue lying between the two layers.

Each ovary is about an inch and a half (38·1 mm.) in length, half an inch (12·7 mm.) in thickness, and three-quarters of an inch (19·1 mm.) in width at its broadest portion. The outer extremity is somewhat rounded and is attached to one of the fimbriæ of the Fallopian tube. The inner extremity is more pointed, and is attached to the side of the uterus by means of the ligament of the ovary. This ligament is shown in Fig. 275 (7, 7). It is a rounded cord, composed of non-striated muscular fibres spread out upon the attached extremity of the ovary and the posterior surface of the uterus, and is covered by peritoneum. The weight of each ovary is sixty to one hundred grains (3·9 to 6·5 grammes), and these organs are largest in the adult virgin. Its attached border is called the hilum; and at this portion the vessels and nerves penetrate. The surface is marked by rounded, translucent elevations, produced by distended Graafian follicles, with little cicatrices indicating the situation of ruptured follicles. There may also be seen, between the distended follicles, corpora lutea in various stages of atrophy.

The surface of the ovaries does not present the appearance of a continuation of the peritoneum. At the base is a distinct line surrounding the hilum, which indicates where the peritoneum ceases and where the proper epithelial covering of the ovary begins; and there is a well-marked and abrupt distinction between the endothelium of the serous surface and the layer of cylindrical cells covering the ovary itself. There seems to be little difference between the cells covering the ovaries and those lining the Fallopian tubes, except that the latter are provided with cilia.

On making a section of the ovary, it is readily seen by the naked eye that the organ is composed of two distinct structures; a cortical substance, formerly called the tunica albuginea, which is about $\frac{1}{25}$ of an inch (1 mm.) in thickness, and a medullary substance containing a large number of blood-vessels. The cortical substance alone contains the Graafian follicles. The external layer of this is denser than the deeper portion, but there is no distinct, fibrous membrane such as is sometimes described under the name of the tunica albuginea.

The cortical substance of the ovary consists of connective tissue in several layers, the fibres of which are continuous with the looser fibres of the medullary portion. In the substance of this layer, are embedded the ova, enclosed in the sacs called Graafian follicles. This layer contains a few blood-vessels, coming from the medullary portion, which surround the follicles.

The medullary portion of the ovary is very vascular and is composed of small bands, or trabeculæ of connective tissue, with non-striated muscular fibres. The blood-vessels, which penetrate at the hilum, are large and convoluted, especially at the hilum itself, where there is a mass of convoluted veins, forming a sort of vascular bulb (Rouget). In the medullary portion of the ovary, which is sometimes called the vascular zone, the muscular fibres follow the vessels, in the form of muscular sheaths.

In addition to the blood-vessels, the ovary receives nerves from the spermatic plexus of the sympathetic, the exact mode of termination of which has not been ascertained. Lymphatics have also been demonstrated at the hilum.

*Graafian Follicles.*—These vesicles, or follicles, were described and figured by DeGraaf, in 1672, and are known by his name. They contain the ova, undergo a series of peculiar changes, enlarge, approach the surface of the ovary, and finally are ruptured, discharging their contents into the fimbriated extremity of the Fallopian tube. The Graafian follicles are developed exclusively in the cortical substance. If the ovary be examined at any period of life, no follicles are found in the medullary substance; but a few of the larger may project downward, so as to encroach somewhat upon it, being actually of a diameter greater than the thickness of the cortex. The entire number of follicles of all sizes in each ovary is about 36,000 (Henle). According to the table of measurements given by Waldeyer, the primordial follicles in the human embryon, at the seventh month, measure $\frac{1}{800}$ to $\frac{1}{250}$ of an inch (30 to 100 $\mu$) in diameter, and the primordial ova, $\frac{1}{1650}$ to $\frac{1}{1000}$ of an inch (15 to 25 $\mu$).

The ovary appears very early in embryonic life, in the form of a cellular outgrowth from the Wolffian body. Most of its cells are small, but as early as the fourth or fifth day, in the chick, some of them are to be distinguished by their large size, their rounded form and the presence of a large nucleus. These cells are supposed to be primordial ova. In the process of development of the ovary some of the peripheral cells penetrate in the form of tubes (the so-called ovarian tubes) and at the same time, delicate processes, formed of connective tissue and blood-vessels, extend from the fibrous stroma underlying the epithelium and enclose collections of cells. It is probable that there are two modes of formation of follicles; one, by the penetration of epithelial tubes from the surface, which become constricted and divided off into closed cavities, and the other, by the extension of fibrous processes from below, which enclose little collections of cells. By both of these processes, little cavities are formed, which contain a number of cells. In each of these cavities, there is a single, large, rounded cell, with a large nucleus, this cell being a primordial ovum; and in addition, in the same cavity, there are other cells, which are the cells of the Graafian follicle. The exact nature of the processes just described has been studied in the chick; but it is probable that the same kind of development occurs in mammalia and in the human subject.

From birth until just before the age of puberty, the cortical substance of the ovary contains several thousands of what are termed primordial follicles, enclosing the primordial ova; and it is probable that after the ovaries are fully developed at birth, no additional ova or Graafian follicles make their appearance. The prevailing idea is, indeed, that the great majority of these never arrive at maturity, and that they undergo atrophy at various stages of their development. In the adult, according to Waldeyer, the smallest Graafian follicles measure $\frac{1}{800}$ to $\frac{1}{600}$ of an inch (30 to 40 $\mu$), and the smallest ova, a little more than $\frac{1}{1000}$ of an inch (26 $\mu$). The primordial ova have the form of rounded cells, each with a large, clear nucleus and a nucleolus. Other structures are developed in and surrounding these cells, as the ova arrive at their full development.

The most important stage in the development of the ova and Graafian follicles is observed at about the period of puberty. At this time a number of follicles (twelve, twenty, thirty or even more) enlarge, so that all sizes are observed, between the smallest primordial follicles, $\frac{1}{800}$ of an inch (30 $\mu$), and the largest, nearly $\frac{1}{2}$ an inch (12 mm.) in diameter. In follicles that have attained any considerable size, there are the fully developed ova, one in each follicle—except in very rare instances, when there are two—and these ova have a diameter of about $\frac{1}{125}$ of an inch (200 $\mu$). In the process which culminates in the discharge of the ovum into the fimbriated extremity of the Fallopian tube, the Graafian follicle gradually enlarges, becomes distended with liquid and finally breaks through and ruptures upon the surface of the ovary.

Fig. 276 shows the follicles and ova of various sizes. It is observed that the larger follicles contain fully formed ova and have a proper, fibrous coat.

The ova here present an epithelial covering and are embedded in a mass of the epithelial lining of the follicle, the membrana granulosa, this mass being called the discus or cumulus proligerus.

At or near the period of their maturity the Graafian follicles present several coats and are filled with an albuminous liquid. The mature follicles

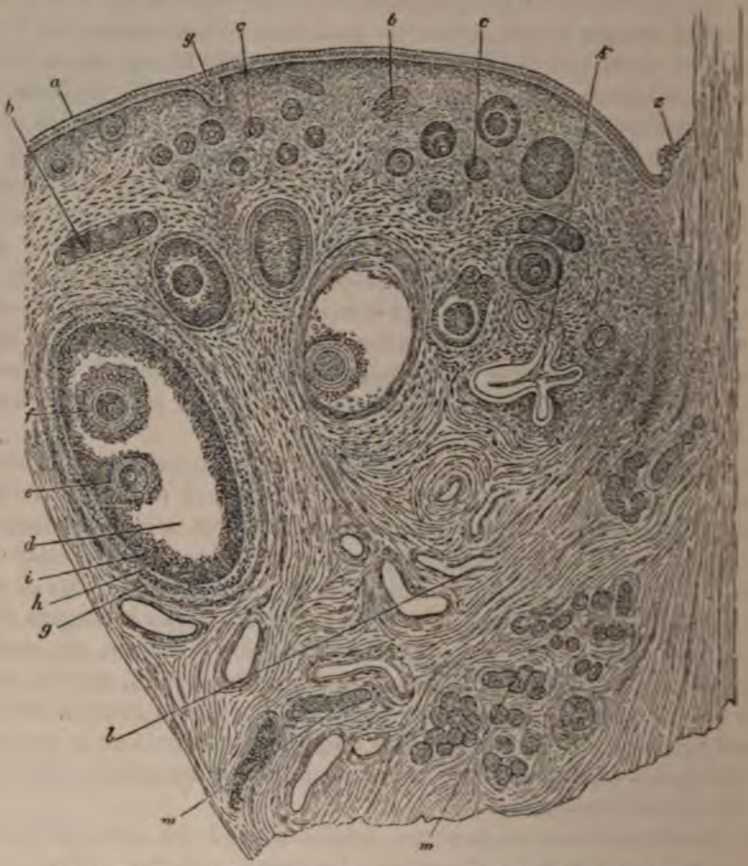

FIG. 276.—*Portion of a sagittal section of the ovary of an old bitch* (Waldeyer).
*a*, ovarian epithelium ; *b*, *b*, ovarian tubes ; *c*, *c*, younger follicles ; *d*, older follicle ; *e*, discus proligerus with the ovum ; *f*, epithelium of a second ovum in the same follicle ; *g*, fibrous coat of the follicle ; *h*, proper coat of the follicle ; *i*, epithelium of the follicle (membrana granulosa) ; *k*, collapsed, atrophied follicle ; *l*, blood-vessels ; *m*, *m*, cell-tubes of the parovarium, divided longitudinally and transversely ; *y*, tubular depression of the ovarian epithelium, in the tissue of the ovary ; *z*, beginning of the ovarian epithelium, close to the lower border of the ovary.

project just beneath the surface and form little, rounded, translucent elevations. The smallest follicles are near the surface, and as they enlarge, at first they become deeper, as is seen in Fig. 276, becoming superficial only as they approach the condition of fullest distention.

Taking one of the largest follicles as an example, two fibrous layers can be distinguished; an outer layer, of ordinary connective tissue, and an inner layer, the tunica propria, formed of the same kind of tissue, with the difference that as the follicle enlarges the inner layer becomes vascular. The vascular tunica propria is lined by cells of epithelium, forming the so-called membrana granulosa. At a certain point in this membrane, is a mass of cells, called the discus or cumulus proligerus, in which the ovum is embedded. The situation of the discus proligerus is not invariable; sometimes it is at the most superficial, and sometimes it is at the deepest part of the Graafian follicle.

The liquid of the Graafian follicle is alkaline, slightly yellowish and not viscid. It contains a small quantity of albuminoid matter, coagulable by heat, alcohol and acids. This liquid is supposed to be secreted by the cells lining the inner membrane of the follicle.

*The Parovarium.*—The parovarium, or organ of Rosenmüller, is simply the remains of the Wolffian body, lying in the folds of the broad ligament, between the ovary and the Fallopian tube. It consists of twelve to fifteen tubes of fibrous tissue, lined by ciliated epithelium. It has no physiological importance.

*The Uterus.*—The form, situation and relations of the uterus and Fallopian tubes have already been indicated and are shown in Fig. 275.

The uterus is a pear-shaped body, somewhat flattened antero-posteriorly, presenting a fundus, a body and a neck. At its lower extremity, is an open-

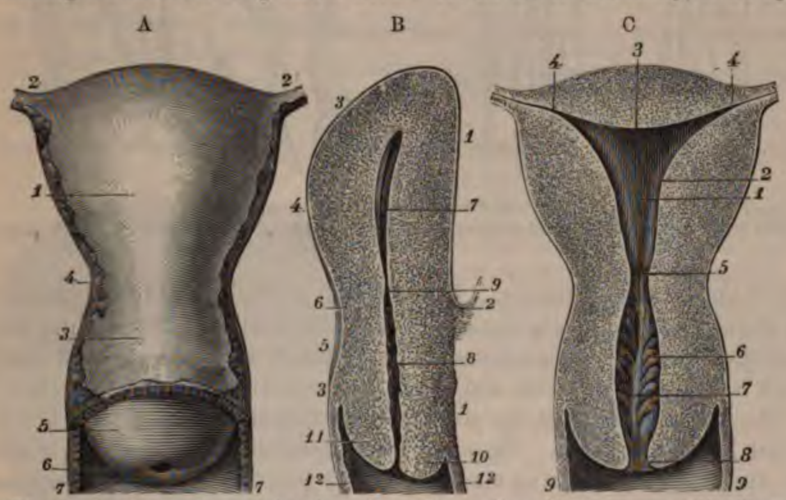


FIG. 277.—*Virgin uterus.* A.—*anterior view.* B.—*median section.* C.—*transverse section* (Sappey).
A. 1. body ; 2, 2, angles ; 3, cervix ; 4, site of the os internum ; 5, vaginal portion of the cervix ; 6, external os ; 7, 7, vagina.
B. 1, 1, profile of the anterior surface ; 2, vesico-uterine *cul-de-sac* ; 3, 3, profile of the posterior surface; 4, body ; 5, neck ; 6, isthmus ; 7, cavity of the body ; 8, cavity of the cervix ; 9, os internum ; 10, anterior lip of the os externum ; 11, posterior lip ; 12, 12, vagina.
C. 1, cavity of the body ; 2, lateral wall ; 3, superior wall ; 4, 4, cornua ; 5, os internum ; 6, cavity of the cervix ; 7, arbor vitæ of the cervix ; 8, os externum ; 9, 9, vagina.

ing into the vagina, called the os externum. At the upper portion of the neck, is a constriction, which indicates the situation of the os internum. The form of the uterus is shown in Fig. 277 (A). It usually is about three inches (76·2 mm.) in length, two inches (50·8 mm.) in breadth at its widest portion, and one inch (25·4 mm.) in thickness. Its weight is one and a half to two and a half ounces (42·5 to 71 grammes). It is somewhat loosely held in place by the broad and round ligaments and by the folds of the peritoneum in front and behind. The delicate layer of peritoneum which forms its external covering extends behind as far down as the vagina, where it is reflected back upon the rectum, and anteriorly, a little below the upper extremity of the neck (os internum), where it is reflected upon the urinary bladder. At the sides of the uterus, the peritoneal covering, a little below the entrance of the Fallopian tubes, becomes loosely attached and leaves a line for the penetra-


FIG. 278.—*Muscular fibres of the uterus* (Sappey).
A, fibres of the uterus of the fœtus at term ; B, of a woman twenty years of age ; C, of a woman just delivered.

tion of the vessels and nerves. Fig. 277 (C), giving a view of the interior of the uterus, shows a triangular cavity, with two cornua corresponding to the openings of the Fallopian tubes, and very thick walls, the greatest part of which is composed of layers and bands of non-striated muscular fibres.

The muscular walls of the uterus are composed of non-striated fibres arranged in several layers. These fibres are spindle-shaped and always nucleated, the nucleus presenting one or two large granules which have been taken for nucleoli. They are closely bound together, so that they are isolated with great difficulty. In addition to an amorphous, adhesive substance between the muscular fibres, there are many rounded and spindle-shaped cells of connective tissue, and a few elastic fibres. The muscular tissue of the uterus is remarkable from the fact that the fibres enlarge immensely during gestation, becoming at that time ten or fifteen times as long and five or six times as broad as they are in the unimpregnated state. They are united into bundles or fasciculi, which in certain of the layers interlace with each other in every direction. The fibres are divided into external, middle and internal layers.

The external, muscular layer, which is very thin but distinct, is closely


FIG. 279.—*Superficial muscular fibres of the anterior surface of the uterus* (Liégeois).
*a, a*, round ligaments; *b, b*, Fallopian tubes; *c, c, c, e, e*, transverse fibres; *d, f*, longitudinal fibres.

attached to the peritoneum. When the uterus is somewhat enlarged after impregnation, there are observed oblique and transverse, superficial fibres passing over the fundus and the anterior and posterior surfaces to the sides. Here they are prolonged upon the Fallopian tubes, the round ligament and the ligament of the ovary, and they also extend between the layers of the broad ligament. This external layer is so thin that it can not be very efficient in the expulsive contractions of the uterus; but from its connections with the Fallopian tubes and the ligaments, it is useful in holding the uterus in place. It does not extend entirely over the sides of the uterus.

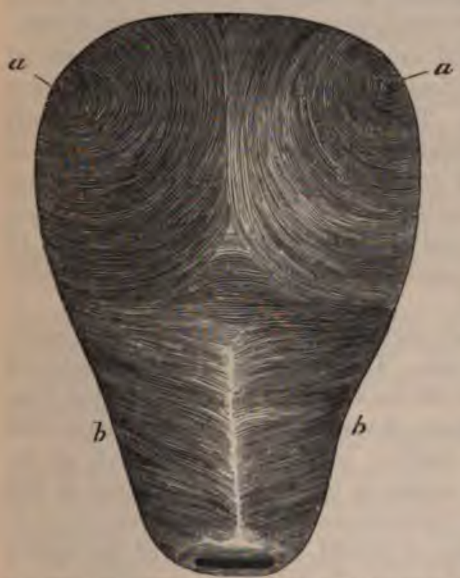


FIG. 280.—*Inner layer of muscular fibres of the uterus* (Liégeois).
*a, a*, rings around the openings of the Fallopian tubes; *b, b*, circular fibres of the cervix.

The middle, muscular layer is the one most efficient in the parturient contractions of the uterus. It is composed of a thick and intricate net-work of fasciculi interlacing with each other in every direction.

The inner, muscular layer is arranged in the form of broad rings, which surround the Fallopian tubes, become larger as they extend over the body of the uterus and meet at the centre of the organ, near the neck.

The mucous membrane of the uterus is of a pale, reddish color; and that portion lining the body is smooth and is so closely attached to the subjacent structures that it can not be separated to any great extent by dissection. There is, indeed, no proper submucous, areolar tissue, the membrane being applied directly to the uterine walls. It is covered by a single layer of cylindrical epithelial cells, with delicate cilia, the movements of which are from without inward, toward the openings of the Fallopian tubes. Examination of the surface of the membrane with a low magnifying power shows the openings of a great number of tubular glands. These glands usually are simple, sometimes branched, dividing, about midway between the opening and the lower extremity, into two and very rarely into three secondary tubules. Their course generally is tortuous, so that their length frequently exceeds the thickness of the mucous membrane. The openings of these tubes are about $\frac{1}{350}$ of an inch (72 $\mu$) in diameter. Their secretion, which forms a thin layer of mucus on the surface of the membrane in health, is grayish, viscid and feebly alkaline. The tubes themselves have very thin, structureless walls and are lined with cylindrical, ciliated epithelial cells.

The changes which the mucous membrane of the body of the uterus undergoes during menstruation are remarkable. Under ordinary conditions its thickness is $\frac{1}{25}$ to $\frac{1}{14}$ of an inch (1 to 1·8 mm.); but it measures during the menstrual period $\frac{1}{6}$ to $\frac{1}{4}$ of an inch (4·2 to 6·4 mm.).

In the cervix the membrane is paler, firmer and thicker than the membrane of the body of the uterus, and between these two mucous surfaces there is a distinct line of demarkation. It is more loosely attached to the subjacent tissue, in the cervix, and the anterior and posterior surfaces of the neck present an appearance of folds radiating from the median line, forming what has been called the arbor vitæ uteri, or plicæ palmatæ. Throughout the entire cervical membrane, are mucous glands, and in addition, in the lower portion, are a few rounded, semi-transparent, closed follicles, called the ovules of Naboth, which are cystic enlargements of obstructed follicles. The upper half of the cervical membrane is smooth but the lower half presents a large number of villi. The epithelium of the cervix presents great variations in its character in different individuals. Before the time of puberty the entire membrane of the cervix is covered with ciliated epithelium. After puberty, however, the epithelium of the lower portion changes its character, and there are cylindrical cells above, with squamous cells in the inferior portion. The latter extend upward in the neck, to a variable distance.

The blood-vessels of the uterus are very large and present certain important peculiarities in their arrangement. The uterine arteries pass between the layers of the broad ligament, to the neck, and then ascend by the sides of the uterus, presenting a rich plexus of vessels, anastomosing above with branches from the ovarian arteries, sending branches over the body of the uterus, and finally penetrating the organ, to be distributed mainly in the middle layer of muscular fibres. In their course these vessels present a convoluted arrangement and form a sort of mould of the body of the uterus. Rouget has called this the erectile tissue of the internal generative organs. It lacks, however, certain of the characters of true, erectile tissue. By placing the pelvis in a bath of warm water and injecting what he called the spongy bodies of the ovaries and uterus, by the ovarian veins, he produced a distention of the vessels and a sort of erection, the uterus executing a movement upward.

In the muscular walls of the uterus, are large veins, the walls of which

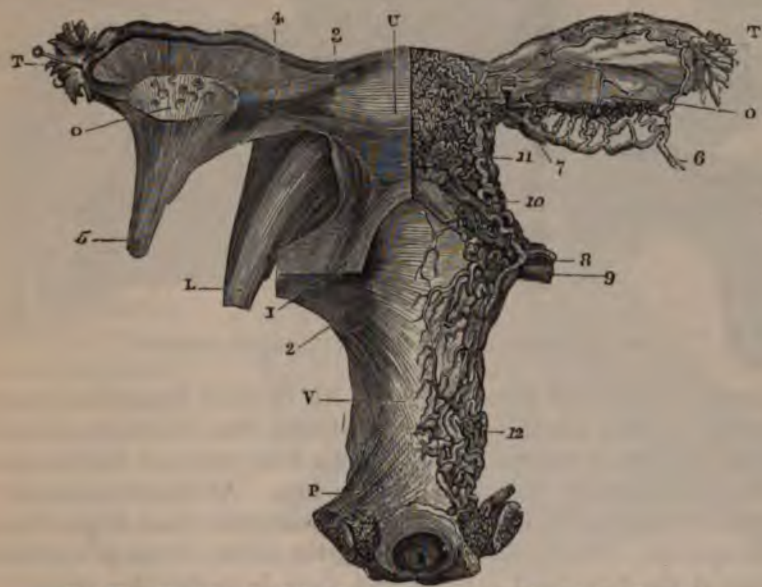


FIG. 281.—*Blood-vessels of the uterus and ovaries; posterior view* (Rouget).
T, T, Fallopian tubes; O, O, ovaries; U, uterus; V, vagina; P, pubis; L, anterior round ligament; 1, 2, muscular fibres of the vagina; 3, 4, ligament of the ovary; 5, superior round ligament; 6, ovarian artery; 7, ovarian vein; 8, uterine artery; 9, uterine vein; 10, 11, uterine plexus; 12, vaginal plexus.

are closely adherent to the uterine tissue. During gestation these vessels become enlarged, forming the so-called uterine sinuses.

Lymphatics are not very abundant in the unimpregnated uterus, but they become largely developed during gestation. They exist in a superficial and a deep layer, the deeper vessels being connected with lymph-spaces in the muscular walls and in the mucous membrane.

The uterine nerves are derived from the inferior hypogastric and the spermatic plexuses, and the third and fourth sacral. In the substance of the uterus they present in their course small collections of ganglionic cells, and it is said that the nerves pass finally to the nucleoli of the muscular fibres (Frankenhaeuser).

*The Fallopian Tubes.*—The Fallopian tubes, or oviducts, lead from the ovaries to the uterus. They are shown in Fig. 275. These tubes are three to four inches (7·6 to 10·1 centimetres) long, but their length is not always equal upon the two sides. They lie between the folds of the broad ligament, at its upper border. Opening into the uterus upon either side at the cornua, they present a small orifice, about $\frac{1}{25}$ of an inch (1 mm.) in diameter. From the cornua they take a somewhat undulatory course outward, gradually increasing in size, so that they are rather trumpet-shaped. Near the ovary they turn downward and backward. The extremity next the ovary is marked by ten to fifteen fimbriæ, or fringes, which have given this the name of the

FIG. 282.—*Section through the right Fallopian tube* (Richard).

fimbriated extremity, or morsus diaboli. All of these fringe-like processes are free except one; and this one, which is longer than the others, is attached to the outer angle of the ovary and presents a little gutter, or furrow, extending from the ovary to the opening of the tube. At this extremity, is the abdominal opening of the tube, which is two or three times larger than the uterine opening. Passing from the uterus, the caliber of the tube gradually increases as the tube itself enlarges, and there is an abrupt constriction at the abdominal opening.

Beneath the peritoneal coat, which is formed by the layers of the broad ligament, is a layer of connective tissue, containing a rich plexus of blood-vessels. This constitutes the proper, fibrous coat of the Fallopian tubes.

The muscular layer is composed mainly of circular fibres of the non-striated variety, with a few longitudinal fibres prolonged over the tube from the external, muscular layer of the uterus. This coat is quite thick and sends bands between the layers of the broad ligament, to the ovary.

The mucous membrane of the tube is thrown into folds, which are longitudinal and transverse near the uterus and are more complicated at the dilated portion. In this portion, next the ovary, embracing about the outer two-thirds, the folds project far into the caliber of the tube. These are sometimes simple, but more frequently they present secondary folds, often meeting as they project from opposite sides. This arrangement gives an arborescent appearance to the membrane on transverse section of the tube. The mucous membrane is covered by cylindrical ciliated epithelium, the movement of the cilia being from the ovary toward the uterus. The membrane of the tubes has no mucous glands.

It is not necessary to give a minute description of the external organs of the female. Opening by the vulva externally, and terminating at the neck of the uterus, is a membranous tube, the vagina. This lies between the bladder and the rectum. It has a curved direction, being about four inches (10 centimetres) long in front, and five to six inches (12·7 to 15·2 centimetres) long posteriorly. At the constricted portion of the outer opening, there is a muscle, called the sphincter vaginæ, and the tube is somewhat narrowed at its upper end, where it embraces the cervix uteri. The inner surface presents a mucous membrane, marked by transverse rugæ, with papillæ and mucous glands. Its surface is covered with flattened epithelium. The vagina is quite extensible, as it must be during parturition, to allow the passage of the child. It presents a proper coat of dense, fibrous tissue, with longitudinal and circular muscular fibres of the non-striated variety. Surrounding it, is a rather loose, so-called erectile tissue, which is most prominent at its lower portion.

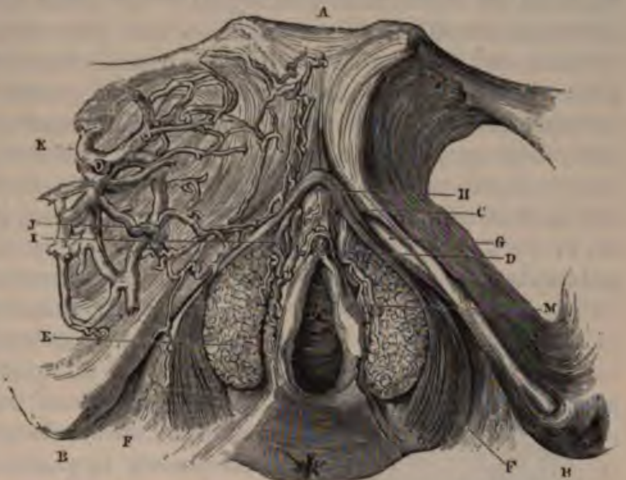

FIG. 283.—*External erectile organs of the female* (Liégeois).

A, pubis; B, B, ischium; C, clitoris; D, gland of the clitoris; E, bulb; F, constrictor muscle of the vulva; G, left pillar of the clitoris; H, dorsal vein of the clitoris; I, intermediary plexus; J, vein of communication with the obturator vein; K, obturator vein; M, labia minora.

The parts composing the external organs are abundantly supplied with vessels and nerves. In the clitoris, which corresponds to the penis of the male, and on either side of the vestibule, there is a true, erectile tissue.

*Structure of the Ovum.*—The ovum lies in the Graafian follicle, embedded in the mass of cells which constitutes the discus proligerus (Von Baer, 1827). Within the discus, surrounding the ovum, there seem to be two kinds of cells; (1) cells evidently belonging to the Graafian follicle and similar to the cells in other parts of the membrana granulosa; (2) a single layer of columnar cells belonging to the ovum and probably concerned in the production of the proper membrane of the ovum, the vitelline membrane. Regarding the vitelline membrane as the external covering, the ovum appears to be composed of (1) a clear, transparent membrane; (2) a granular mass (the vitellus) filling this membrane completely; (3) a large, clear nucleus, called the germinal vesicle; and (4) a nucleolus, called the germinal spot.

The diameter of the ripe ovum, in the human subject and in mammals, is about $\frac{1}{125}$ of an inch (200 $\mu$), and its form is globular. The external membrane of the ovum is clear, marked by fine, transverse lines, quite strong and resisting, and measures about $\frac{1}{2500}$ of an inch (10 $\mu$) in thickness. It appears as a transparent ring in the mass of cells in which the ovum is embedded, and forms what is called the zona pellucida. The primordial ovum has at first no special, investing membrane; but as it develops, it presents, surrounding the vitellus, a single layer of columnar cells. At the deepest portion of these cells, a homogeneous basement-membrane is gradually formed, and the cells undergo a sort of cuticular transformation, becoming finally the vitelline membrane.

An important point, in this connection, is the question of the existence of pores, or perforations in the vitelline membrane. As will be seen farther on, there can be no doubt with regard to the actual penetration of the spermatozoids through this membrane, so that they come in contact with the vitellus; and it is in this way that the ovum is fecundated. In the osseous fishes and in mollusks, there seems to be no question with regard to the existence of a number of pores in the vitelline membrane; but these are not easily demonstrated in the ova of mammals. Admitting the existence of a micropyle and pores in the vitelline membrane in fishes and mollusks, it is certain that openings are very much more indistinct, if they can be seen at all, in the ova of mammals; but the fact of the actual penetration of spermatozoids almost of necessity presupposes the presence of orifices. It must be difficult, in examining a perfectly transparent and homogeneous membrane in water, which would fill up all pores, to distinguish any openings, and their presence is to be admitted, mainly because the spermatozoids are known to pass through. The idea of their existence in mammals certainly receives support from analogy with the lower forms of animals.

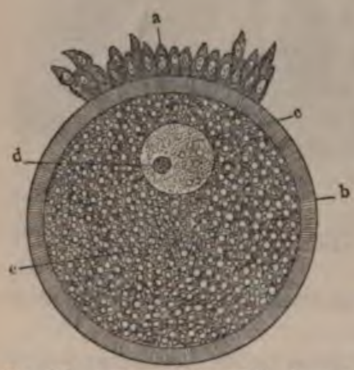


FIG. 284.—*Ovum of the rabbit, from a Graafian follicle $\frac{1}{10}$ of an inch (2 mm.) in diameter* (copied from Waldeyer and reduced).

*a*, epithelium of the ovum; *b*, zona pellucida, with radiating striations (vitelline membrane); *c*, germinal vesicle; *d*, germinal spot; *e*, vitellus.

The vitellus contains the elements which are to undergo development into the embryon. It is composed of a semi-fluid mass, containing, in addition to the germinal vesicle, large numbers of granules. Some of these granules are large, strongly refracting, globular bodies, which are so bright and so abundant that they obscure the other parts of the vitellus. Between these, are many albuminoid granules, which are much smaller and not so distinct.

The germinal vesicle, sometimes called the vesicle of Purkinje, is the enlarged nucleus of the primordial ovum. It is a clear, globular vesicle, about $\frac{1}{550}$ of an inch ($45\,\mu$) in diameter, embedded in the vitellus, its position varying in different ova. It presents in its interior a number of fine granules, and a large, dark spot, called the germinal spot, or the spot of Wagner, which measures about $\frac{1}{3600}$ of an inch ($7\,\mu$) in diameter. This spot corresponds to the nucleolus of the primordial ovum. In mammals the mature ovum contains but one germinal vesicle and one germinal spot.

*Discharge of the Ovum.*—A ripe Graafian follicle measures $\frac{3}{8}$ to $\frac{1}{2}$ of an inch (10 to 12 mm.) in diameter, and presents a rounded elevation, containing a plexus of blood-vessels, upon the surface of the ovary. At its most prominent portion, is an ovoid spot in which the membranes are entirely free from blood-vessels. At this spot, which is called the macula folliculi, the coverings finally give way and the contents of the follicle are discharged. For a short time anterior to the rupture of the follicle, important changes have been going on in its structure. In the first place, the non-vascular portion situated at the very surface of the ovary undergoes fatty degeneration, by which this part of the wall gradually becomes weakened. At the same time, at the other portions of the follicle, there is a proliferation of cells which project into the interior, and an extension, into the interior, of blood-vessels in the form of loops. These changes, with an increase in the pressure of liquid and the fatty degeneration of the macula, cause the follicle to burst; and with the liquid, the discus proligerus and the ovum are expelled. The formation of a cell-growth in the interior of the follicle is the beginning of the corpus luteum; and this occurs some time before the discharge of the ovum takes place.

The time at which the follicle ruptures, particularly with reference to the menstrual period, is not definite; but it is certain that while sexual excitement probably hastens the discharge of an ovum by producing a greater or less tendency to congestion of the internal organs, ovulation takes place independently of the action of coition. The opportunities for determining this fact in the human female are not frequent; but it has been fully demonstrated by observations upon the inferior animals, and there is now no doubt with regard to the identity of the phenomena of rut and of menstruation. At stated periods marked by the phenomena of menstruation, one Graafian follicle—and sometimes more than one—becomes distended and usually ruptures and discharges its contents into the Fallopian tubes. This discharge of an ovum or ova may occur at the beginning, at the end, or at any time during the continuance of the menstrual flow. Upon this point the observations of Coste seem entirely conclusive. In a woman who died on the first day of menstruation, he found a recently ruptured follicle; in other instances, at a more advanced period and toward the decline of the menstrual flow, he found evidences that the rupture had occurred later; in the case of a female who drowned herself four or five days after the cessation of the menses, a follicle was found in the right ovary, so distended that it was ruptured by very slight pressure; and other instances were observed in which follicles were not ruptured during the menstrual period.

## Passage of Ova into the Fallopian Tubes.

The fact that the ova in the great majority of instances pass into the Fallopian tubes is sufficiently evident. The fact, also, that ova may fall into the cavity of the peritoneum is illustrated by the occasional occurrence of extraüterine pregnancy, a rare accident, which shows that in all probability the failure of unimpregnated ova to enter the tubes is exceptional. As regards the mechanism of the passage of the ova into the tubes, however, the explanation is difficult. At the present time there are two theories with regard to this process; one, in which it is supposed that the fimbriated extremities of the Fallopian tubes, at the time of rupture of the Graafian follicles, become adapted to the surface of the ovaries; and the other, that the ova are carried to the openings of the tubes by ciliary currents. Neither of these theories, however, is susceptible of actual demonstration; and their value is to be judged from anatomical facts. It is not difficult to understand, taking into account the situation of the ovaries and the relations of the Fallopian tubes, how an ovum may pass into the tube, without invoking the aid of muscular action. It may be supposed, for example, that a Graafian follicle is ruptured when the fimbriated extremity of the tube is not applied to the surface of the ovary. One of the fimbriæ, longer than the others, is attached to the outer angle of the ovary and presents a little furrow, or gutter, leading to the opening of the tube. This furrow is lined by ciliated epithelium, as indeed, is the mucous membrane of all of the fimbriæ, the movements of which produce a current in the direction of the opening, which would apparently be sufficient to carry the ovum into the tube. At the same time there probably is a constant flow of liquid over the ovarian surface, directed by the ciliary current toward the tube; and when the liquid of the ruptured follicle is discharged this, with the ovum, takes the same course (Becker). This probably is the mechanism of the passage of the ova into the Fallopian tubes; and it is possible that the fimbriated extremity may be drawn toward the ovarian surface, although it is difficult to understand how it can be closely applied to the ovary and exert any considerable pressure upon the distended follicle. It is proper to note, also, that the conditions dependent upon the currents of liquid directed by the movements of cilia are constant and could influence the passage of an ovum at whatever time it might be discharged, while a muscular action would be more or less intermittent.

*Puberty and Menstruation.*—At a certain period of life, usually between the ages of thirteen and fifteen, the human female undergoes a remarkable change and arrives at what is termed the age of puberty. At this time there is a marked increase in the general development of the body; the limbs become fuller and more rounded; a growth of hair makes its appearance upon the mons Veneris; the mammary glands increase in size and take on a new stage of development; Graafian follicles enlarge, and one or more approach the condition favorable to rupture and the discharge of ova. The female becomes capable of impregnation, and continues so, in the absence of pathological conditions, until the cessation of the menses.

The age of puberty is earlier in warm than in cold climates; and many instances are on record in which the menses have appeared exceptionally much before the usual period. Generally at the age of forty or forty-five, the menstrual flow becomes irregular, occasionally losing its sanguineous character, and it usually ceases at about the age of fifty years. It is said that sometimes the menses return, with a second period of fecundity, though this is rare. According to most writers, while climate has a certain influence over the time of cessation as well as the first appearance of the menses, this is not very marked. When the menses appear early in life, they usually cease at a correspondingly early period; but this is by no means constant. There are, also, many exceptions to the ordinary limits to the period of fecundity.

Although there is a periodical condition of heat in the lower animals, connected with ovulation, a sanguineous discharge from the genital organs is not often observed. It is only in monkeys that there is a counterpart of what occurs in the human female; and observations upon these animals have shown that they are subject to a monthly discharge of blood, at this time giving evidence of unusual salacity.

In the human female, near the time of puberty, there is sometimes a periodical, sero-mucous discharge from the genital organs, preceding, for a few months, the regular establishment of the menstrual flow. Sometimes, also, after the first discharge of blood, the female passes several months without another period, when the second flow takes place and the menses then become regular. In a condition of health the periods recur every month, until they cease, at what is termed the change of life. In the majority of cases the flow recurs on the twenty-seventh or the twenty-eighth day; but sometimes the interval is thirty days. As a rule, also, utero-gestation, lactation, and severe diseases, acute and chronic, suspend the periods; but this has exceptions, as some females menstruate regularly during pregnancy, and it is not very uncommon for the menses to appear during lactation.

Removal of the ovaries, especially when this occurs before the age of puberty, usually is followed by arrest of the menses. It is a well known fact that animals do not present the phenomena of heat, after extirpation of the ovaries. Raciborski has quoted cases of this operation in the human subject, in which the menses were arrested; but this rule does not appear to be absolute, as Storer has reported at least one case, in which menstruation continued with regularity for more than a year after removal of both ovaries. Thomas, in three cases of removal of both ovaries from menstruating women, which he followed for five and a half months to two years and eleven months after the operation, noted no return of menstruation; but in one case, nearly six months after the operation, the patient had "a bloody discharge from the vagina and all the symptoms accompanying the menstrual function." Other cases of this kind are on record.

When a cow gives birth to twins, one a male and the other apparently a female, the latter is called a free-martin and generally has no ovaries. John Hunter, in his paper on the free-martin, gave a full description of this anomalous animal and stated that it does not breed or show any inclination for the bull. In an examination of a free-martin, raised and killed by the late Prof. James R. Wood, in 1868, the uterus was found rudimentary and there were no ovaries (Flint).

A menstrual period presents three stages: first, invasion; second, a sanguineous discharge; third, cessation.

The stage of invasion is variable in different females. There is usually, anterior to the establishment of the flow, more or less of a feeling of general *malaise*, a sense of fullness and weight in the pelvic organs, accompanied with a greater or less increase in the quantity of vaginal mucus, which becomes brownish or rusty in color and has a peculiar odor. At this time, also, the breasts become slightly enlarged. This stage may continue for one or two days, although in many instances the first evidence of the access of a period is a discharge of blood.

When the symptoms above indicated occur, the general sense of uneasiness usually is relieved by the discharge of blood. During this, the second stage, blood flows from the vagina in variable quantity, and the discharge continues for three to five days. With regard to the duration of the flow there are great variations in different individuals. Some women present a flow of blood for only one or two days; while in others the flow continues for five to eight days, within the limits of health. A fair average, perhaps, is four days.

It is difficult to arrive at even an approximation of the total quantity of the menstrual flow. Burdach estimated it at five to six ounces (about 150 to 175 grammes). According to Longet this estimate is rather low, the quantity ordinarily ranging between ten and twelve ounces (300 and 350 grammes), occasionally amounting to seventeen ounces (500 grammes), or even more. It is well known that the quantity is very variable, as is the duration of the flow; and the difficulties in the way of estimating the total discharge are evident.

The characters of the menstrual flow are sufficiently simple. Supposing the discharge to continue for four days, on the first day the quantity is comparatively small; on the second and third the flow is at its height; and the quantity is diminished on the fourth day. During this, the second stage, the fluid has the appearance of pure, arterial blood, not coagulated, and mixed, as has been shown by microscopical examination, with epithelium from the vagina, cylindrical cells from the uterus, leucocytes and a certain quantity of sero-mucous secretion. Chemical examinations of the fluid have not shown any marked peculiarities, except that the quantity of fibrin is either not estimated or is given as much less than in ordinary blood.

The mechanism of the hæmorrhage is probably the same as in epistaxis. There is a rupture of small blood-vessels, probably capillaries, and blood is thus exuded from the entire surface of the membrane lining the uterus and sometimes from the membrane of the Fallopian tubes. The blood is then discharged into the vagina and is kept fluid by the vaginal mucus. The mucus of the body of the uterus is viscid and alkaline; the mucus secreted at the neck is gelatinous, viscid and tenacious, and is also alkaline; the vaginal mucus is decidedly acid, creamy and not viscid, containing epithelium and leucocytes.

The third stage, that of cessation of the menses, is very simple. During the latter part of the second stage the flow of blood gradually diminishes. The discharge becomes rusty, then lighter in color, and in the course of about twenty-four hours, it assumes the characters observed in the intermenstrual period.

When the menstrual flow has become fully established there is no very marked general disturbance, except a sense of lassitude, which may become exaggerated if the discharge be unusually abundant. It has been noted, however, by Rabuteau, that during the menstrual period the production of urea is diminished more than twenty per cent., that the pulse becomes slower and that the temperature falls at least one degree Fahr. (about half a degree C.).

If the mucous membrane of the uterus be examined during the menstrual flow, it is found smeared with blood, which sometimes extends into the Fallopian tubes. It is then much thicker and softer than during the intermenstrual period. Instead of measuring about $\frac{1}{14}$ of an inch (1·8 mm.) in thickness, as it does under ordinary conditions, its thickness is $\frac{1}{6}$ to $\frac{1}{4}$ of an inch (4·2 to 6·4 mm.). It becomes more loosely attached to the subjacent parts, is somewhat rugous, and the glands are very much enlarged. At the same time there are developed, in the substance of the membrane, large numbers of spherical and fusiform cells. This condition probably precedes the discharge of blood by several days, during which time the membrane is gradually preparing for the reception of the ovum. There is also a fatty degeneration of the different elements entering into the structure of the mucous membrane, including the blood-vessels, this change being most marked at the surface; and it is on account of the weakened condition of the vascular walls that the hæmorrhage takes place. A short time after the flow has ceased, the mucous membrane returns to its ordinary condition. There is a considerable desquamation of epithelium from the uterus, with the flow of blood, during the menstrual period. Sometimes, in normal menstruation, the epithelium thrown off is in the form of patches.

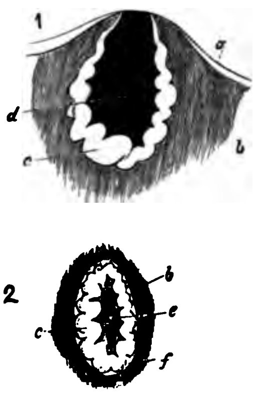

FIG. 285.—*Sections of two corpora lutea; natural size* (Kölliker).
1, corpus luteum eight days after conception; *a*, external coat of the ovary; *b*, stroma of the ovary; *c*, convoluted wall of the Graafian follicle; *d*, clot of blood.
2, corpus luteum at the fifth month of pregnancy; *b*, stroma of the ovary; *c*, convoluted wall of the Graafian follicle; *e*, decolorized clot; *f*, fibrous envelope of the corpus luteum.

*Changes in the Graafian Follicles after their Rupture* (*Corpus Luteum*).—After the discharge of an ovum, its Graafian follicle undergoes certain retrograde changes, involving the formation of what is called the corpus luteum. Even when the discharged ovum has not been fecundated, the corpus luteum persists for several weeks, so that, ovulation occurring every month, several of these bodies, in various stages of retrogression, may sometimes be seen in the ovaries.

For a certain time anterior to the discharge of the ovum, there is a cell-proliferation from the proper coat of the Graafian follicle, and probably from the membrana granulosa, with a projection of looped blood-vessels into the interior of the follicle. This is the first formation of the corpus luteum. At the time of rupture of the follicle, the ovum, with a great part of the membrana granulosa, is discharged. Usually, at the time of rupture of the follicle, there is a discharge of blood into its interior; but this is not invariable, although there is always a gelatinous exudation more or less colored with blood. At the same time the follicular wall undergoes hypertrophy, and it becomes convoluted, or folded, and highly vascular. This convoluted wall, formed by the proper coat of the follicle, is surrounded by the fibrous tunic, and its thickening is most marked at the deepest portion of the follicle. At the end of about three weeks, the body—which is now called the corpus luteum, on account of its yellowish or reddish-yellow color—has arrived at its maximum of development and measures about half an inch (12·7 mm.) in depth, by about three-quarters of an inch (19·1 mm.) in length, its form being ovoid. The convoluted wall then contains a layer of large, pale, finely granular cells, which are internal and are supposed to be the remains of the epithelium of the follicle. The great mass of this wall, however, is composed of large, nucleated cells, containing fatty globules and granules of reddish or yellowish pigmentary matter. The thickness of the wall is about one-eighth of an inch (3·2 mm.) at its deepest portion.

After about the third week the corpus luteum begins to contract; its central portion and the convoluted wall become paler; and at the end of seven or eight weeks, a small cicatrix marks the point of rupture of the follicle.

The above are the changes which occur in the Graafian follicles after their rupture and the discharge of ova, when the ova have not been fecundated; and the bodies thus produced are called false corpora lutea, as distinguished from corpora lutea formed after conception, which latter are called true corpora lutea.

*Corpus Luteum of Pregnancy.*—When a discharged ovum has been fecundated, the corpus luteum passes through its various stages of development and retrogression much more slowly than the ordinary corpus luteum of menstruation. The retrogression begins toward the end of the third month. "During the fourth month, the corpus luteum diminishes by nearly a third, and toward the end of the fifth, it ordinarily is reduced one-half. It still forms, however, during the first days after parturition, and in the greatest number of cases, a tubercle which has a diameter of not less than $\frac{2}{7}$ to $\frac{1}{3}$ of an inch (7·3 to 8·5 mm.). The tubercle afterward diminishes quite rapidly; but it is nearly a month before it is reduced to the condition of a little, hardened nucleus, which persists more or less as the last vestige of a process so slow in arriving at its final term. Nevertheless, there is nothing absolute in the retrograde progress of this phenomenon. I have seen women, dead at the sixth and even the eighth month of pregnancy, present corpora lutea as voluminous as others at the fourth month" (Coste, 1849). The differences between the corpora lutea of pregnancy and of menstruation were accurately described by Dalton, in 1851 and 1877.

## Male Organs of Generation.

The chief physiological interest attached to the anatomy of the male organs of generation relates to the testicles, which are the organs in which the male element of generation is developed. As regards the penis, it will be necessary to do little more than describe the mechanism of erection and of the ejaculation of semen.

*The Testicles.*—The testicles are two symmetrical organs, situated, during a certain period of intraüterine life, in the abdominal cavity, but finally descending into the scrotum. Immediately beneath the skin of the scrotum, is a loose, reddish, contractile tissue, called the dartos, which forms two distinct sacs, one enveloping each testicle, the inner portion of these sacs fusing in the median line, to form a septum. Within these two sacs the coverings of each testicle are distinct. These organs are suspended in the scrotum, by the spermatic cords, the left usually hanging a little lower than the right. The coverings for each testicle, in addition to those just mentioned, are the intercolumnar fascia, the cremaster muscle, the infundibuliform fascia, the tunica vaginalis and the proper, fibrous coat.

The tunica vaginalis is a shut sac of serous membrane, covering the testicle and epididymis and reflected from the posterior border of the testicle to the wall of the scrotum, lining the cavity occupied by the testicle on either side and also extending over the spermatic cord. This tunic is really a process of peritoneum, which has become shut off from the general lining of the abdominal cavity. The spermatic cord is composed of the vas deferens, blood-vessels, lymphatics and nerves, with the coverings already described which expand and surround the testicle.

Beneath the tunica vaginalis are the testicles, with their proper, fibrous coat. These organs are ovoid, and flattened laterally and posteriorly. "They are an inch and a half to two inches (38·1 to 50·8 mm.) long, about an inch and a quarter (31·8 mm.) from the anterior to the posterior border, and nearly an inch (25·4 mm.) from side to side. The weight of each varies from three-quarters of an ounce to an ounce (21·2 to 28·3 grammes), and the left is often a little the larger of the two" (Quain). The proper, fibrous coat is everywhere covered by the closely adherent tunica vaginalis, except at the posterior border, where the vessels enter and the duct passes out. At the outer edge of this border, is the epididymis, formed of convoluted tubes, presenting a superior enlargement, called the globus major, a long mass running the length of the testicle, called the body, and a smaller, inferior enlargement, called the globus minor. This too is covered with the tunica vaginalis. Between the membrane covering the testicle and epididymis and the layer lining the scrotal cavity, is a small quantity of serum, just enough to moisten the serous surfaces. At the superior portion of the testicle are one or more small, ovoid bodies, called the hydatids of Morgagni, each attached to the testicle, by short, constricted processes. These have no physiological importance and are supposed to be the remains of fœtal structures.

The proper, fibrous coat of the testicle is called the tunica albuginea. It is white, dense, inelastic, measures about $\frac{1}{25}$ of an inch (1 mm.) in thickness, and is simply for the protection of the contained structures. Sections of the testicle, made in various directions, show an incomplete, vertical process of the tunica albuginea, called the corpus Highmorianum or the mediastinum testis. This is wedge-shaped, about $\frac{1}{6}$ of an inch (4·2 mm.) wide at its superior and thickest portion, is pierced by a number of openings, and lodges blood-vessels and seminiferous tubes. From the mediastinum, delicate, radiating processes of connective tissue pass to the inner surface of the tunica albuginea, dividing the substance of the testicle into imperfect lobules, which lodge the seminiferous tubes. The number of these lobules has been estimated at one hundred and fifty to two hundred. Their shape is pyramidal, the larger extremities presenting toward the surface, with the pointed extremities situated at the mediastinum.

Lining the tunica albuginea and following the mediastinum and the processes which penetrate the testicle, is a tunic, composed of blood-vessels and delicate, connective tissue, called the tunica vasculosa, or pia mater testis.

Lodged in the cavities formed by the trabeculæ of connective tissue, are the seminiferous tubes, in which the male elements of generation are developed. These tubes exist to the number of about eight hundred and forty in each testicle and constitute almost the entire substance of the lobules. The larger lobules contain five or six tubes, the lobules of median size, three or four, and the smallest enclose sometimes but a single tube. Each tube presents a convoluted mass, which can be disentangled under water, particularly if the testicle be macerated for several months in water with a little nitric acid. The entire length of the tube when thus unravelled is about thirty inches (7·6 decimetres), and its diameter is $\frac{1}{200}$ to $\frac{1}{150}$ of an inch (125 to 166 $\mu$). It begins by two to seven short, blind extremities and sometimes by anastomosing loops. The cæcal diverticula are usually found in the external half of the tube, and their length is $\frac{1}{12}$ to $\frac{1}{8}$ of an inch (2·1 to 3·2 mm.). The anastomoses are sometimes between the tubes of different lobules, sometimes between tubes in the same lobule and sometimes between different points in the same tube. As the tubes pass toward the posterior portion of the testicle, they unite into about twenty straight canals, called the vasa recta, about $\frac{1}{75}$ of an inch (0·33 mm.) in diameter, which penetrate the mediastinum testis. In the mediastinum the tubes form a close net-work, called the rete testis; and at the upper

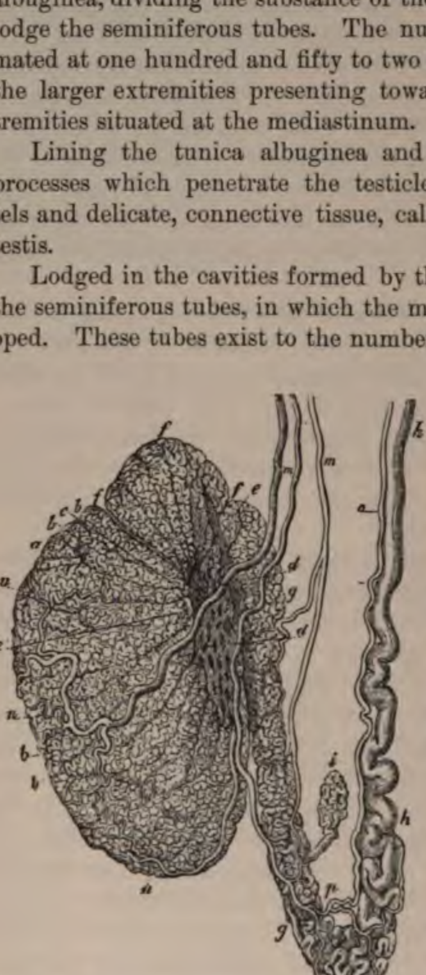

FIG. 286.—*Testicle and epididymis of the human subject* (Arnold).

*a*, testicle · *b*, *b*, *b*, *b*, lobules of the testicle ; *c*, *c*, vasa recta ; *d*, *d*, rete testis ; *e*, *e*, vasa efferentia ; *f*, *f*, *f*, cones of the globus major of the epididymis ; *g*, *g*, epididymis ; *h*, *h*, vas deferens ; *i*, vas aberrans ; *m*, *m*, branches of the spermatic artery, to the testicle and epididymis ; *n*, *n*, *n*, ramification of the artery upon the testicle ; *o*, deferential artery ; *p*, anastomosis of the deferential with the spermatic artery.

portion of the posterior border they pass out of the testicle, by twelve to fifteen openings, and are here called the vasa efferentia.

Having passed out of the testicle, the vasa efferentia form a series of small, conical masses, which together constitute the globus major, or head of the epididymis. Each of these tubes when unravelled is six to eight inches (15 to 20 centimetres) long, gradually increasing in diameter, until they all unite into a single, convoluted tube, which forms the body and the globus minor of the epididymis. This single tube of the epididymis, when unravelled, is about twenty feet (6 metres) in length.

The walls of the seminiferous tubes in the testicle itself are composed of connective tissue and of peculiar structures which will be fully described in connection with the processes of development of the spermatozoids. In the rete testis it is uncertain whether the tubes have a special fibrous coat or are simple channels in the fibrous structure. They are here lined with pavement-epithelium. In the vasa efferentia and the epididymis, there is a fibrous membrane, with longitudinal and circular fibres of non-striated muscular tissue and a lining of ciliated epithelium. The movements of the cilia are toward the vas deferens. In the lower portion of the epididymis the cilia are absent. The tubular structures of the testicle, the epididymis and the beginning of the vas deferens are shown in Fig. 286.

At the lower portion of the epididymis, communicating with the canal, there usually is found a small mass, formed of a convoluted tube of variable length, called the vas aberrans of Haller (*i*, Fig. 286). This is sometimes wanting.

*Vas Deferens.*—The excretory duct of the testicle extends from the epididymis to the prostatic portion of the urethra and is a continuation of the single tube which forms the body and globus minor of the epididymis. It is somewhat tortuous near its origin, and it becomes larger at the base of the bladder, just before it is joined by the duct of the seminal vesicle. Near its point of junction with this duct it becomes narrower. Its entire length is nearly two feet (about 6 decimetres).

The course of the vas deferens is in the spermatic cord, to the external abdominal ring, through the inguinal canal, to the internal ring, where it leaves the blood-vessels, passes beneath the peritoneum, to the side of the bladder, then along the base of the bladder, by the inner side of the seminal vesicle, finally joining the duct of the seminal vesicle, the common tube forming the ejaculatory duct, which opens into the prostatic portion of the urethra.

The walls of the vas deferens are thick, abundantly supplied with vessels and nerves, and provided with an external, fibrous, a middle, muscular, and an internal, mucous coat. The greater part of that portion of the tube which is connected with the bladder is dilated and sacculated. The fibrous coat is composed of strong, connective tissue. The muscular coat presents three layers; an external, rather thick layer of longitudinal fibres, a thin, middle layer of circular fibres, and a thin, internal layer of longitudinal fibres, all of the non-striated variety. By the action of these fibres the vessel may be made to undergo energetic, peristaltic movements, and this has followed stimulation of that portion of the spinal cord corresponding to the fourth lumbar vertebra, which is described by Budge as the genito-spinal centre.

The mucous membrane of the vas deferens is pale, thrown into longitudinal folds in the greatest part of the canal, and presents a number of additional rugæ in the sacculated portion, these rugæ enclosing little, irregularly polygonal spaces. The membrane is covered with columnar epithelium, which is not ciliated. In the sacculated portion are large numbers of mucous glands.


FIG. 287.—*Vas deferens, vesiculæ seminales and ejaculatory ducts* (Liégeois).
*a*, vas deferens; *b*, seminal vesicle; *c*, ejaculatory duct; *d*, termination of the ejaculatory duct; *e*, opening of the prostatic utricle; *f*, *g*, veru montanum; *h*, *l*, prostate.

Attached to the vas deferens, near the head of the epididymis, is a little mass of convoluted and sacculated tubes, called the organ of Giraldès, or the corpus innominatum. The body is $\frac{1}{6}$ to $\frac{1}{3}$ of an inch (4·2 to 8·5 mm.) long and $\frac{1}{12}$ of an inch (2·1 mm.) broad. Its tubes are lined with cells of pavement-epithelium, which often are filled with fatty granules. Generally the tubes present only blind extremities, but some of them occasionally communicate with the tubes of the epididymis. This part has no physiological importance. It was regarded by Giraldès as the remnant of the Wolffian body, analogous to the parovarium.

*Vesiculæ Seminales.*—Attached to the base of the bladder and situated externally to the vasa deferentia, are the two vesiculæ seminales. These bodies are each composed of a coiled and sacculated tube, four to six inches (10 to 15 centimetres) in length when unravelled, and somewhat convoluted, in the natural state, into an ovoid mass which is firmly bound to the vesical wall. The structure of the seminal vesicles is not very unlike that of the sacculated portion of the vasa deferentia. They have an external, fibrous coat, a middle coat of muscular fibres, and a mucous lining. Muscular fibres pass over these vesicles from the bladder, both in a longitudinal and in a circular direction, and serve as compressors, by the action of which their contents may be discharged. The mucous coat is pale, finely reticulated, and covered with cells of polygonal epithelium, which are nucleated and contain brownish granules. The vesiculæ seminales undoubtedly serve, in part at least, as receptacles for the seminal fluid, as their contents often present a greater or less number of spermatozoids. Although the membrane of the vesicles seems to produce an independent secretion, the presence of mucous glands has not been demonstrated.

The ejaculatory ducts are formed by the union of the vasa deferentia with the ducts of the vesiculæ seminales on either side, and they open into the prostatic portion of the urethra. Except that their coats are much thinner, they have essentially the same structure as the vasa deferentia.

*Prostate.*—Surrounding the vesical extremity of the urethra, including what is known as its prostatic portion, is the prostate gland, or body. This organ, except as it secretes a fluid which forms a part of the ejaculated semen, has chiefly a surgical interest, so that it is unnecessary to describe minutely its form and relations. It is enveloped in a very dense, fibrous coat, contains many glandular structures opening into the urethra, and presents a great number of non-striated, with a few striated muscular fibres, some just beneath the fibrous coat and others penetrating its substance and surrounding the glands.

The glands of the prostate are most distinct at that portion which lies behind the urethra. In the posterior portion of this canal are found about twenty openings, which lead to tubes ramifying in the glandular substance. These tubes are formed of a structureless membrane branching as it penetrates the gland. They present hemispherical diverticula in their course, and terminate in dilated extremities, which are looped and coiled. In the deeper portions of the tubes, the epithelium is columnar or cubical, becoming tessellated near their openings, and sometimes laminated.

The prostatic fluid probably is secreted only at the moment of ejaculation. Its characters will be considered in connection with the composition of the seminal fluid. According to Kraus the prostatic fluid has an important office in maintaining the vitality of the spermatozoids. "The spermatozoa, in the absence of the prostatic fluid, can not live in the mucous membrane of the uterus of mammalia; but with its aid they may live for a long time in the uterine mucus, often more than thirty-six hours."

*Glands of the Urethra.*—In front of the prostate, opening into the bulbous portion of the urethra, are two small, racemose glands, called the glands of Méry or of Cowper. These have each a single excretory duct, are lined throughout with cylindrical epithelium, and secrete a viscid, mucus-like fluid, which forms a part of the ejaculated semen. Sometimes there exists only a single gland, and occasionally, though rarely, both are absent. Their uses are probably not very important.

The glands of Littre, found throughout the entire urethra and most abundant on its anterior surface, are simple racemose glands, extending beneath the mucous membrane into the muscular structure, presenting here four or five acini. As these acini are surrounded by muscular fibres, it is easy to understand how their secretion may be pressed out during erection of the penis. They are lined throughout with columnar or conoidal epithelium, and secrete a clear and somewhat viscid mucus, which is mixed with the ejaculated semen.

## Male Elements of Generation.

The spermatozoids are the essential, male elements of generation, and these are produced in the substance of the testicle, by a process analogous to that of the development of other true, anatomical elements. The testicles can not be regarded strictly as glandular organs. They are analogous to the ovaries, and they are the only organs in which spermatozoids can be developed, as the ovaries are the only organs in which the ovum can be formed. If the testicles be absent, the power of fecundation is lost, none of the fluids secreted by the accessory organs of generation being able to perform the office of the true, fecundating elements.

In the healthy male, at the climax of a normal venereal orgasm, 11·6 to 92·6 grains (0·75 to 6 grammes) of seminal fluid are ejaculated with considerable force from the urethra, by an involuntary, muscular spasm (Montegazza). This fluid requires about four days for its complete restoration. The semen is slightly mucilaginous, grayish or whitish, streaked with lines more or less opaque, and it evidently contains various kinds of mucus. It has a faint and peculiar odor, *sui generis*, which is observed only in the ejaculated fluid and not in any of its constituents examined separately. It is a little heavier than water and does not mix with it or dissolve. After ejaculation it becomes jelly-like and dries into a peculiar, hard mass, which may be softened by the application of appropriate liquids. The liquid is not coagulated by heat and does not contain albumen. Its reaction is faintly alkaline. It contains in the human subject 100 to 120 parts of solid matter per 1,000.

The chemical constitution of the semen has not been very thoroughly investigated and does not present the same physiological importance as its anatomical characters. Aside from the anatomical elements derived from the testicles and the genital passages, it presents an organic substance (spermatine) which has nearly the same chemical characters as ordinary mucine. It also contains a considerable quantity of phosphates. During desiccation, elongated, rhomboidal crystals make their appearance, frequently arranged in groups, which are supposed to be derived from the prostatic fluid and to consist of phosphoric acid combined with an organic base, the formula for which, united with hydrochloric acid, is $C_2H_3NHCl$ (Schreiner). These are sometimes called spermatic crystals.

In the dilated portion of the vasa deferentia the mucous glands secrete a fluid which is the first that is added to the spermatozoids as they come from the testicles. This fluid is brownish or grayish. It contains epithelium, and small, rounded granulations, which are dark and strongly refractive. The liquid itself is very slightly viscid. In the vesiculæ seminales there is a more abundant secretion of the grayish fluid, with epithelium, small, colorless concretions of nitrogenized matter, called by Robin, sympexions, and a few leucocytes. The glandular structures of the prostate produce a creamy secretion with fine granulations. It is chiefly to the admixture of this fluid that the semen owes its whitish appearance. Finally as the semen is ejaculated, it receives the viscid secretion of the glands of Cowper, a certain quantity of stringy mucus from the follicles of the urethra, with perhaps a little of the urethral epithelium.

Anatomically considered the seminal fluid contains no important elements except the spermatozoids, the various secretions just mentioned serving simply as a vehicle for the introduction of these bodies into the generative passages of the female.

*Spermatozoids.*—In August, 1677, a German student, named Von Hammen, discovered the spermatozoids in the human semen and exhibited them to Leeuwenhoek, who studied them as closely as was possible with the instruments at his command. For a long time they were regarded as living animalcules, although now they are considered simply as peculiar, anatomical elements endowed with movements, like ciliated epithelium. These elements are developed within the seminiferous tubes; and they differ, not so much in their mode of development, as in their form, in different animals.

FIG. 288.—*Spermatozoids, spermatic crystals, leucocytes etc.* (Peyer).

The fluid taken from the vesiculæ seminales of an adult who has died suddenly or the ejaculated semen contains, in addition to the various accidental or unimportant anatomical elements that have been mentioned, innumerable bodies, resembling animalcules, which present a flattened, conoidal head and a long, tapering, filamentous tail. The tail is in active motion, and the spermatozoids move about the field of view with considerable rapidity and force, pushing aside little corpuscles or granules with which they may come in contact. Under favorable conditions, particularly in the generative passages of the female, the movements may continue for several days.

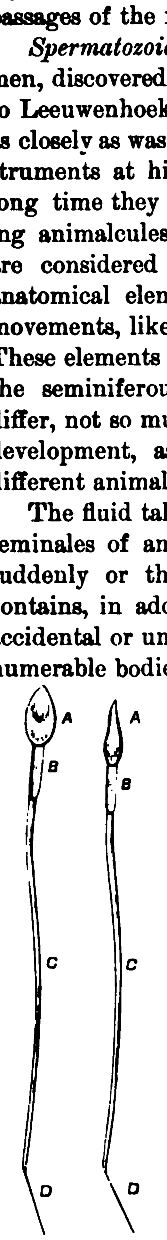


FIG. 289. — *Human spermatozoids; magnified 600 diameters* (Landois).
1, flat view; 2, side view; A A, head; B B, intermediate segment; C C, tail; D D, terminal filament.

Microscropical examination does not reveal any very distinct structure in the substance of the spermatozoids. The head is about $\frac{1}{5000}$ of an inch (5 $\mu$) long, $\frac{1}{8000}$ of an inch (3 $\mu$) broad, and $\frac{1}{25000}$ of an inch (1 $\mu$) in thickness. The tail is about $\frac{1}{500}$ of an inch (50 $\mu$) in length. La Vallette St. George has found in man and many of the inferior animals the "intermediate segment" described first by Schweigger-Seidel, though he does not agree with Schweigger-Seidel that this portion is motionless. The length of the intermediate segment is about $\frac{1}{4000}$ of an inch (6 $\mu$). It usually is described as the beginning of the tail; and the only difference between this and other portions is that it is a little thicker. At the extreme end, is a short and excessively fine filament, called the terminal filament.

Water speedily arrests the movements of the spermatozoids, which may be restored by the addition of dense, saline and other solutions. All of the alkaline, animal fluids of moderate viscidity favor the movements, while the action of acid or of very dilute solutions is unfavorable. The movements are suspended by extreme cold, but they return when the ordinary temperature is restored.

Before the age of puberty the seminiferous tubes are much smaller than in the adult, and they contain small, transparent cells, which in their form and arrangement resemble epithelium. As puberty approaches, however, the tubes become larger, and the contents change their character. The walls are then provided with spindle-shaped cells with a nucleated, protoplasmic lining, sending prolongations into the interior of the tube. These prolongations afterward break up into little, rounded bodies called spermatoblasts, a part of each one of which becomes the head of a spermatozoid (Ebner). Between the prolongations, are the so-called spermatic cells. The spermatoblasts send out each one a short process which forms the intermediate seg-


FIG. 290.—*Spermatogenesis; semi-diagrammatic* (Landois).

I, transverse section of a seminal tubule; A, external membrane; B, protoplasmic lining; C, spermatoblast; S, seminal cells.
II, projection with F, spermatoblasts; S, seminal cells.
III, spermatoblasts with spermatozoids not yet detached.
IV, spermatoblasts with a spermatozoid detached.

ment of the spermatozoid, and from this a long filament is developed, which forms the tail. The spermatozoid is detached when its development is complete.

The spermatozoids are motionless while they are within the testicle, the epididymis or the vasa deferentia, apparently on account of the density of the substance in which they are embedded; for movements are sometimes presented when the contents of the vasa deferentia are examined with the addition of water or of saline solutions. Once in the vesiculæ seminales, and for a certain time after ejaculation, the spermatozoids are in active motion. When the spermatozoids have ceased their movements they are incapable of fecundating the ovum.

The semen, thus developed and mixed with the various secretions before mentioned, is found during adult life and sometimes even in advanced age, and under physiological conditions it contains innumerable spermatozoids in active movement; but if sexual intercourse be frequently repeated at short intervals, the ejaculated fluid becomes more and more transparent,

**homogeneous and scanty, and it may consist of a small quantity of secretion from the vesiculæ seminales and the glands opening into the urethra, without spermatozoids and consequently deprived of fecundating properties.**

**In old men the seminal vesicles may not contain spermatozoids; but this is not always the case, even in very advanced life. Instances are constantly occurring of men who have children in their old age, in which the paternity of the offspring can hardly be doubted. Duplay, in 1852, examined the semen of a number of old men, and found, in about half the number, spermatozoids, normal in appearance and quantity, though in some the vesiculæ seminales contained either none or very few. Some of the persons in whom the spermatozoids were normal were between seventy-three and eighty-two years of age. These observations were confirmed by Dieu, who found spermatozoids in a man eighty-six years of age. The contents of the seminal vesicles, in these cases, were examined twenty-four hours after death. Some of the subjects died of acute, and others, of chronic diseases; but the mode of death did not present any differences in the cases classed with reference to the presence of spermatozoids. As the result of his own and of other recorded observations, Dieu concluded that the power of fecundation often persists for a considerable time after copulation has become impossible on account simply of absence of the power of erection.**

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## CHAPTER XXV.

### *FECUNDATION AND DEVELOPMENT OF THE OVUM.*

**General considerations—Fecundation—Changes in the fecundated ovum—Segmentation of the vitellus—Primitive trace—Blastodermic layers—Formation of the membranes—Amniotic fluid—Umbilical vesicle—Formation of the allantois and the permanent chorion—Umbilical cord—Membranæ deciduæ—Formation of the placenta—Uses of the placenta—Development of the ovum—Development of the cavities and layers of the trunk in the chick—Vertebral column—Development of the skeleton—Development of the muscles—Development of the skin—Development of the nervous system—Development of the organs of special sense—Development of the digestive apparatus—Development of the respiratory apparatus—Development of the face—Development of the teeth—Development of the genito-urinary apparatus—Development of the circulatory apparatus—Description of the fœtal circulation.**

As far as the male is concerned, coitus is rendered possible by erection of the penis. This may occur before puberty, but at this time intercourse can not be fruitful. Coitus may be impossible in old age, from absence of the power of erection; but spermatozoids may still exist in the vesiculæ seminales, and fecundation might occur if the seminal fluid could be discharged into the generative passages of the female. Coitus may take place in the female before the age of puberty or after the final cessation of the menses, but intercourse can not then be fruitful. There are many instances of conception following what would be called imperfect intercourse, as in cases of unruptured hymen, deformities of the male organs, etc., which show that the actual penetration of the male organ is not essential, and that fecundation may occur provided the seminal fluid find its way into even the lower part of the vagina. Conception has also followed intercourse when the female has been insensible or entirely passive. Unlike certain of the lower animals, the human subject presents no distinct periodicity in the development of the spermatozoids; but in reiterated connection, an orgasm may occur when the ejaculated fluid has no fecundating properties.

With regard to the mechanism of erection, little remains to be said after the description that has been given of true, erectile tissue, in connection with the physiology of the circulation. The cavernous and spongy bodies of the penis usually are taken as the type of erectile organs. In these parts the arteries are large, contorted, provided with unusually thick, muscular coats, and are connected with the veins by vessels considerably larger than the true capillaries. They are supported by a strong, fibrous net-work of trabeculæ, which contains non-striated muscular fibres; so that when the blood-vessels are completely filled the organ becomes enlarged and rigid. Researches with regard to the nerves of erection show that the vessels of erectile tissues are distended by an enlargement of the arterioles of supply, and that there is not simply a stasis of blood produced by constriction of the veins, except possibly for a short time during the period of greatest excitement. In experiments upon dogs Eckhard discovered a nerve derived from the sacral plexus, stimulation of which produced an increase in the flow of blood through the penis, attended with all the phenomena of erection. This nerve arises by two roots, at the sacral plexus, from the first to the third sacral nerves, and is connected with the genito-spinal centre, in the lower part of the lumbar region of the spinal cord (Budge). In the experiments referred to, by a comparison of the quantity of venous blood coming from the penis before and during the stimulation of the nerve, Eckhard found a great increase during erection. It is probable that in addition to the arterial dilatation, when the penis attains its maximum of rigidity there is a certain degree of obstruction to the outflow of blood, by compression of the veins, and that the rigidity is increased by contraction of the trabecular, muscular fibres of the corpora cavernosa. At the climax of an orgasm, the semen is forcibly discharged from the urethra, by spasmodic contractions of the vesiculæ seminales and the ejaculatory muscles. Although this is the physiological mechanism of a seminal discharge, friction of the parts, which usually precedes ejaculation, is not absolutely necessary, as is shown by the occurrence of orgasm during sleep, which is liable to take place in healthy men after prolonged continence.

There are some females, in whom the generative function is performed, even to the extent of bearing children, who have no actual knowledge of a true venereal orgasm; but there are others who experience an orgasm fully as intense as that which accompanies ejaculation in the male. There is, therefore, the important difference in the sexes, that preliminary excitement and an orgasm are necessary to the performance of the generative act in the male, but are not essential in the female. Still there can be scarcely a doubt that venereal excitement in the female facilitates conception, other conditions being favorable. When excitement occurs in the female there is engorgement of the true erectile tissues and possibly of the convoluted vessels surrounding the internal organs. The neck of the uterus becomes hardened and slightly elongated (Wernich); and it has been observed by Litzmann and others, that there occurs a sudden opening and closing of the os, which exerts more or less suction force. These conditions, however, are not essential to fecundation, although they may exert a favorable influence upon the penetration of spermatozoids and may at certain times determine the rupture of a Graafian follicle.

The spermatozoids, once within the cervix uteri, and in contact with the alkaline mucus, which increases the activity of their movements, may pass through the uterus into the Fallopian tubes, and even to the surface of the ovaries. Precisely how their passage is effected, it is impossible to say. It can only be attributed to the movements of the spermatozoids themselves, to capillary action, and to a possible peristaltic action of the muscular structures; but these points have not as yet been subjects of positive demonstration. As regards the human female, it is impossible to give a definite idea of the time required for the passage of the spermatozoids to the ovaries or for the descent of the ovum into the uterus; and it is readily understood how these questions hardly admit of experimental investigation. It is known, however, that spermatozoids reach the ovaries, and they have been seen in motion on their surface, seven or eight days after connection.

*Fecundation.*—The ordinary situation at which the ovum is fecundated is the dilated or external portion of the Fallopian tube. All authorities are agreed that fecundation does not take place in the cavity of the uterus. In rabbits, when the ovum has descended into the uterus, it is surrounded with a dense, albuminous coating which the spermatozoids can not penetrate (Coste). It is possible that this occurs in the human subject. Cases of abdominal pregnancy show that an ovum may be fecundated on the ovary, as soon as it is discharged from the Graafian follicle.

The question of the duration of vitality of the spermatozoids, after their passage into the uterus, has an important bearing upon the time when conception is most liable to follow sexual intercourse. The alkaline mucus of the internal organs actually favors their movements; the movements are not arrested by contact with menstrual blood; and, indeed, when the spermatozoids are mixed with the uterine mucus, they simply change their medium, and there is no reason to believe that they may not retain their vitality as well as in the mucus of the vesiculæ seminales. It seems impossible, therefore, to fix any limit to the vitality of these anatomical elements, under physiological conditions; and it is not certain that spermatozoids may not remain in the Fallopian tubes and around the ovary, when intercourse has taken place immediately after a menstrual period, until the ovulation following. There is an idea, based upon rather general and indefinite observation, that conception is most likely to follow an intercourse which occurs soon after a monthly period; but it is certain that it may occur at any time. It is probable that during the unusual sexual excitement which the female generally experiences after a monthly period, the action of the internal organs, attending and following coitus, presents the most favorable conditions for the penetration of the fecundating elements, and this may explain the more frequent occurrence of conception as a consequence of intercourse at this time.

*Union of the Male with the Female Element of Generation.*—The first important step toward a positive knowledge of the mechanism of fecundation was the discovery of the spermatozoids, in 1677; the second was the demonstration, by Spallanzani, in his experiments upon artificial fecundation, that when the seminal fluid is carefully filtered, the liquid which passes through has no fecundating properties, the male element remaining on the filter; and the third was the demonstration of the presence of spermatozoids within the vitelline membrane.

In the ova of certain animals, an opening, called a micropyle, has been demonstrated in the vitelline membrane (Barry, Keber). This has been seen in the ova of rabbits, although its existence is to be inferred, only, in the human ovum. In the ova of the nephelis vulgaris, or common leech, Robin has seen spermatozoids, to the number of several hundreds, penetrate the vitelline membrane, always at one point, continuing their movements upon the surface of the vitellus. "Almost always, when the penetration has ceased, a bundle of spermatozoids is arrested in the micropyle." The penetration of spermatozoids has been observed in the ova of other animals, including the rabbit (Newport, Coste, Bischoff, Weil and others). Weil has seen spermatozoids wedged in the substance of the zona pellucida, has added blood to a specimen under observation, and has restored the movements of the spermatozoids while in this position. He has also seen, in some instances, perfectly formed spermatozoids in the very substance of the vitellus. As the spermatozoids pass to the vitellus, there is a retraction of its substance, leaving a space between it and the vitelline membrane, which soon becomes filled with a clear liquid.

FIG. 291.—*Ovum of the nephelis vulgaris, showing penetration of spermatozoids and retraction of the vitellus; magnified 300 diameters* (Robin).

All direct observations upon the lower forms of animals have shown that several spermatozoids are necessary for the fecundation of a single ovum; but physiologists have no definite idea of the number required in mammals, much less in the human subject. It is not known what becomes of the spermatozoids after they have come in contact with the vitellus. All that can be said upon this point is that there probably is a direct union between the two generative elements, soon to be followed by the series of changes involved in the first processes of development.

There are many questions connected with hereditary transmission, which if they were susceptible of any thing approaching a positive, scientific explanation, would be of great interest and might appropriately be discussed in a work upon physiology; but although the facts of hereditary influence, as regards the inheritance both of physiological and morbid attributes and tendencies, the influence of the maternal mind upon the development of the fœtus, the effects of previous pregnancies, etc., can not be doubted, their consideration would involve little more than a mere enumeration of remarkable phenomena.

The first question which naturally arises relates to the conditions which determine the sex of the offspring. Statistics show clearly enough the proportions between male and female births; but nothing has ever been done in the way of procreating male or female children at will. According to Longet the proportion of male to female births is about 104 to 105, these figures presenting certain modifications under varying conditions of climate, season, nutrition etc. It has been shown, by very extensive observations upon certain of the inferior animals, that the preponderance of sex in births bears a certain degree of relation to the vigor and age of the parents; and that old and feeble females fecundated by young and vigorous males produce a greater number of males, and *vice versâ;* but no exact laws of this kind have been found applicable to the human subject. The idea that one testicle produces males, and the other, females, or that the two ovaries have distinct offices in this regard, has no foundation in fact; for men with one testicle or females with a single ovary produce offspring of both sexes.

No definite rule can be laid down with regard to the transmission of mental or physical peculiarities to offspring. Sometimes the progeny assumes more the character of the male than of the female parent, and sometimes the reverse is the case, without any reference to the sex of the child; sometimes there appears to be no such relation; and occasionally peculiarities are observed, derived apparently from grandparents. This is true with regard to pathological as well as physiological peculiarities, as in the inherited tendencies to certain diseases, malformations etc.

A peculiar and, it seems to be, an inexplicable fact is that previous pregnancies have an influence upon offspring. This is well known to breeders of animals. If pure-blooded mares or bitches have been once covered by an inferior male, in subsequent fecundations the young are likely to partake of the character of the first male, even if they be afterward bred with males of unimpeachable pedigree. What the mechanism of the influence of the first conception is, it is impossible to say; but the fact is incontestable. The same influence is observed in the human subject. A woman may have, by a second husband, children who resemble a former husband, and this is particularly well marked in certain instances by the color of the hair and eyes. A white woman who has had children by a negro may subsequently bear children to a white man, these children presenting some of the unmistakable peculiarities of the negro race.

Superfecundation of course does not come in the category of influences just mentioned. It is not infrequent to observe twins, when two males have had access to the female, which are entirely distinct from each other in their physical character; a fact which is readily explained by the assumption that two ova have been separately fecundated. This view is entirely sustained by observation and experiment. Many cases illustrating this point are on record.

The following communication, with a photograph, was received in January, 1869, from Dr. John H. Janeway, Assistant Surgeon, U. S. A., and it illustrates superfecundation in the human subject; or at least that was the view taken by the negro father:

"Frances Hunt, a freedwoman, aged thirty-five years, gave birth to twins, February 4, 1867, in New Kent County, Virginia. One of these twins was black, the other was white. Frances is a mulatto. The black child is much darker than she is. Previous to the parturition, she had given birth to seven children, all single births. She was living at the time of her impregnation in the family of a white man as house-servant, sleeping with a black man at night. She insists, however, that she never had carnal intercourse with a white man. She probably does this because the black man turned her out of

FIG. 292.—*Mulatto mother with twins, one white and the other black* (from a photograph).

his house when he saw that one of the children was white. The only negro feature in the white child was its nose. There, its resemblance to its mother was perfect. Its hair was long, light, and silky. Complexion brilliant."

Reference has already been made to the curious fact that when a cow produces twins, one male and the other female, the female, which is called a free-martin, is sterile and presents an imperfect development of the internal organs of generation. This has led to the idea that possibly the same law may apply to the human subject, in cases of twins, one male and the other female; but many observations are recorded in gynæcological works, showing the incorrectness of this view.

It has long been a question whether impressions made upon the nervous system of the mother can exert an influence upon the fœtus in utero. While many authors admit that violent emotions experienced by the mother may affect the nutrition and the general development of the fœtus, some writers of authority deny that the imagination can have any influence in producing deformities. The remarkable cases recorded as instances of deformity due to the influence of the maternal mind are not entirely reliable; and it often happens that when a child is born with a deformity, the mother imagines she can explain it by some impression received during pregnancy, which she recalls only after she knows that the child is deformed. There is, indeed, no satisfactory evidence that the maternal mind has anything to do with the production of deformities in utero.

## Changes in the Fecundated Ovum.

It is probable that the ovum is fecundated either just as it enters the Fallopian tube or in the dilated portion, near the ovary. As it passes down the tube, whether it be or be not fecundated, it becomes covered with an albuminous layer. This layer probably serves to protect the fecundated ovum, and when the spermatozoids do not penetrate the vitelline membrane near the ovary, it presents an obstacle to their passage. Shortly after fecundation the germinal vesicle disappears; but this occurs in ova that have not been fecundated. Soon after ovulation, also, the vitellus gradually withdraws itself from certain portions of the vitelline membrane, or becomes deformed, and then often rotates upon itself. The deformation and gyration of the vitellus, however, have been observed in ova before fecundation. They are of the class of movements called amœboid.

After the penetration of spermatozoids and their union with the vitellus, at least in many of the lowest forms of animals, the appearance of the vitellus undergoes a remarkable change, by which ova that are about to pass through the first processes of development may readily be distinguished from those which have not been fecundated. This change consists in an enlargement of the granules and their more complete separation from the clear substance of the vitellus. The granules then refract light more strongly than before, so that the fecundated ova are distinctly brighter than the others. This is the first appearance that is distinctive of fecundation.

*Polar Globule.*—The next process observed in the ovum is the separation from the vitellus, of a comparatively clear, rounded mass, called by Robin the polar globule. This body has been observed by various anatomists and described under different names. The exact mode of its formation has been studied by Robin in some of the lower forms of animals. The following are the phenomena observed in the ova of the nephelis octoculata:

Five hours after the entrance of the spermatozoids, a little elevation appears at one point in the vitellus. This is the beginning of the polar globule. It increases in size gradually, and becomes constricted at its base, until it is attached to the vitellus by a little pedicle. There is then usually a second globule formed just behind the first, in the same manner; and sometimes a third makes its appearance. As soon as the globules are perfectly formed, they all become detached from the vitellus, but remain adherent to each other, gradually fusing to form a single, rounded, very faintly granular mass. It is opposite this globule that the first furrow of segmentation of the vitellus is observed. The complete formation of the polar globules and their fusion into one occupy three hours. It is probable that the polar globule is formed in the mammalia in the manner above indicated. Sometimes the polar globule is formed in ova that have not been fecundated.

*Vitelline Nucleus.*—A short time after the complete formation of the polar globule, the germinal vesicle having disappeared, the deformed vitellus resumes its original, rounded appearance and fills again the cavity of the vitelline membrane. At this time the extreme periphery of the vitellus becomes clearer, the granules collect in a large zone around the centre, and in the centre itself, a clear, rounded body makes its appearance, which is called the nucleus of the vitellus. This mass is viscid, amorphous, without granules, and is entirely different from the germinal vesicle, having no nucleus at first, a nucleus and a nucleolus, however, appearing in each of the many cells which result from its segmentation. The formation of the nucleus of the vitellus is positive evidence of fecundation. It appears fifteen to thirty hours after penetration of the spermatozoids.

*Segmentation of the Vitellus.*—Almost immediately following the phenomena just described, the vitellus begins to undergo the process of segmentation, by which it is divided into a large number of small cells. This process may take place to a limited extent in non-fecundated ova; but in these instances the cells soon disappear, as the disintegration of the ovum advances. The true segmentation of the vitellus, however, results in the formation of

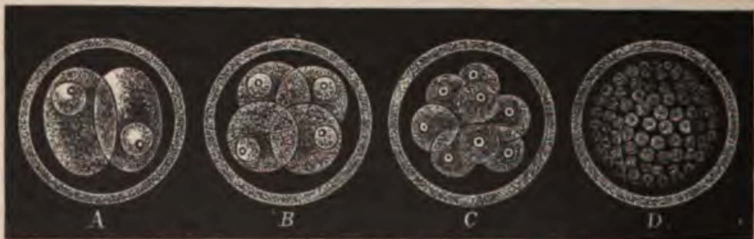


FIG. 293.—*Segmentation of the vitellus* (Haeckel).
A, the vitellus divided into two cells: B, the two cells divided into four; C, the four cells divided into eight; D, the blastodermic cells.

what are called the blastodermic cells. As segmentation has been studied in the inferior animals, there appears first a furrow in the vitellus, at the site of the polar globule, and there is then a furrow on the opposite side, both deepening until the entire vitellus is divided into two globes. These are at first spherical; but they soon become flattened upon each other, into two hemispheres. There follows then a similar division into four, another into eight, and so on, until the entire vitellus is divided into small cells. It is probable that at first the cells of the vitellus have no membrane; but a membrane is soon formed, a nucleus and a nucleolus appear, and the cells are perfect. The ovum is then called the morula. The cells measure $\frac{1}{1250}$ to $\frac{1}{1000}$ of an inch (20 to 25 $\mu$) in diameter.

Most of the phenomena of segmentation have been observed in the lower forms of animals; but there can be no doubt that analogous processes take place in the human ovum. In the rabbit, forty-five and a half hours after copulation, Weil observed an ovum with sixteen segmentations, situated in the lower third of the Fallopian tube. He observed an ovum, ninety-four hours after copulation, with a delicate mosaic appearance, presenting a small, rounded eminence on its surface. It is impossible to say how long the process of segmentation continues in the human ovum. It is stated that it is completed in rabbits in a few days, and in dogs, that it occupies more than eight days (Hermann).

When the cells of the blastoderm are completely formed, they present a polygonal appearance, as they are pressed against the vitelline membrane, their inner surface being rounded. The ovum then contains within the external layer of cells a certain quantity of liquid, and is increased in size to the diameter of $\frac{1}{50}$ to $\frac{1}{25}$ of an inch (0·5 to 1 mm.). It is probably in this condition that the ovum passes from the Fallopian tube into the uterus, at about the eighth day after fecundation.

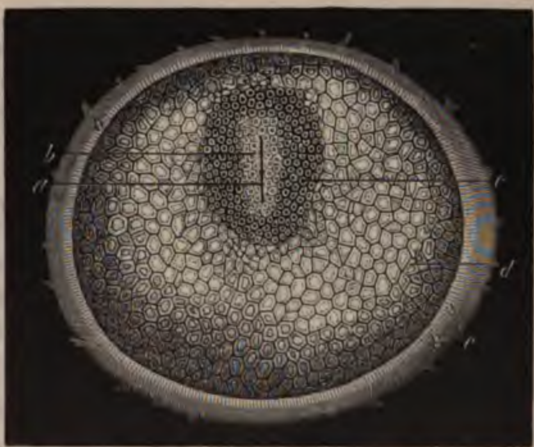

FIG. 294.—*Primitive trace of the embryon* (Liégeois).
*a*, primitive trace; *b*, area pellucida; *c*, area opaca; *d*, blastodermic cells; *e*, *e*, villi beginning to appear on the vitelline membrane.

*Primitive Trace.*—The cells formed by the segmentation of the vitellus, after this process is completed, are arranged in the form of a membrane (the blastodermic membrane) which is farther subdivided, as development advances, into layers, which will be described hereafter. The albuminous covering which the ovum has received in the upper part of the Fallopian tube gradually liquefies and penetrates the vitelline membrane, furnishing, it is thought, matter for the nourishment and development of the vitellus. In the Fallopian tube, indeed, the adventitious albuminous covering of the ovum presents an analogy to the albuminous coverings which the eggs of oviparous animals receive in the oviducts; with the difference that this albuminous matter is almost the sole source of nourishment in the latter, and exists in large quantity, while in viviparous animals, the quantity is small, is generally consumed as the ovum passes into the uterus, and in the uterus, the ovum forms attachments to and draws its nourishment from the vascular system of the mother.

Soon after the formation of the single, blastodermic membrane, at a certain point on its surface there appears a rounded elevation or heap of smaller cells, forming a distinct spot, called the embryonic spot. As development advances, this spot becomes elongated and oval. It is then surrounded by a clear, oval area, called the area pellucida, and the area pellucida is itself surrounded by a zone of cells, more granular and darker than the rest of the blastoderm, called the area opaca. The line thus formed and surrounded by the area pellucida is called the primitive trace. This primitive trace, or primitive groove, however, is a temporary structure. After the groove is formed, there appears in front of but not continuous with it, a new fold and a groove leading from it. This is the "head-fold," and the groove is the true medullary groove, which is subsequently developed into the neural canal.

*Blastodermic Layers.*—The blastodermic cells, resulting originally from the segmentation of the vitellus, are first split apparently into two layers, the external, or epiblast, and the internal, or hypoblast. The epiblast is developed into the epidermis and its appendages, the glands of the skin, the brain and spinal cord, the organs of special sense and possibly some parts of the genito-urinary apparatus. The hypoblast is developed into the epithelium lining the mucous membrane and glands of the stomach and intestinal canal. There is a thickening of both of these layers at the line of development of the cerebro-spinal system, with a furrow that is finally enclosed by an elevation of the ridges and their union posteriorly, forming the canal for the spinal cord.

As the spinal canal is developed, a new layer of cells is formed between the epiblast and the hypoblast, which is called the mesoblast. The mesoblast itself afterward splits into two layers. All the parts not enumerated as developed from the epiblast or hypoblast are developed from the two layers of the mesoblast. The cells lining the vessels, including the lymphatics, which exist in a single layer, are called endothelial cells. This name is also applied to the cells lining the serous membranes.

## Formation of the Membranes.

In the mammalia a portion of the blastoderm is developed into membranes by which a communication and union are established between the ovum and the mucous membrane of the uterus. From the ovum two membranes are developed; one non-vascular, the amnion, and another, the allantois, which is vascular. The two layers of decidua are formed from the mucous membrane of the uterus. At a certain part of the uterus, a vascular connection is established between the mucous membrane and the allantois, and the union of these two structures forms the placenta. The fœtal portion of the placenta is connected with the fœtus, by the vessels of the umbilical cord, and the maternal portion is connected with the great uterine sinuses.

The external covering of the ovum, during the first stage of its development, is the vitelline membrane. As the ovum is received into the uterus, the vitelline membrane develops upon its surface little villosities, which are non-vascular and are formed of amorphous matter with granules. These are the first villosities of the ovum, and they assist in fixing the egg in the uterine cavity. They are not permanent, they do not become developed into the vascular villosities of the chorion and they disappear as the true membranes of the embryon are developed from the blastodermic layers. The vitelline membrane disappears soon after the passage of the ovum into the uterus, when it is replaced by the amnion.

*Formation of the Amnion.*—As the ovum advances in its development, it is observed that a portion of the blastoderm becomes thickened, forming the epiblast, the two layers of the mesoblast and the hypoblast. At about the time when this thickening begins, a fold of the epiblast and of the external layer of the mesoblast makes its appearance, which surrounds the thickened portion and is most prominent at the cephalic and the caudal extremity of the furrow for the neural canal. This fold increases in extent as development advances, passes over the dorsal surface of the embryon and finally meets so as to enclose the embryon completely. At a certain period of the development of the amnion, this membrane consists of an external layer, formed of the external layer of the fold, and an internal layer; and the point of union of the two layers, or the point of meeting of the fold, is marked by a membranous septum.

The two amniotic layers are formed in the way just described, and a complete separation finally takes place, by a disappearance of the septum formed by the meeting of the folds over the back of the embryon. This process occupies four or five days, in the human ovum. The point where the folds meet is called the amniotic umbilicus. When the amnion is thus completely formed, the vitelline membrane has been encroached upon by the external amniotic layer and disappears, leaving this layer of the amnion as the external covering of the ovum. At this time there is a growth of villosities upon the surface of the external amniotic layer, which, like the villosities of the vitelline membrane, are not vascular.

Soon after the development of the amnion the allantois is formed. This membrane is vascular. It encroaches upon and takes the place of the external amniotic membrane, and is covered with hollow villi, which take the place of the villi of the amnion. Over a certain portion of the membrane the villi are permanent. The mode of development of the amnion is illustrated by the diagrammatic Fig. 295. This figure illustrates the formation of the amnion, the umbilical vesicle and the allantois. The last two structures are derived from the hypoblast and the internal layer of the mesoblast.

When the allantois has become the chorion, or the external membrane of the ovum, having taken the place of the external layer of the amnion, the structures of the ovum are the following: 1. The chorion, formed of the two layers of the allantois and penetrated by blood-vessels. 2. The umbili-

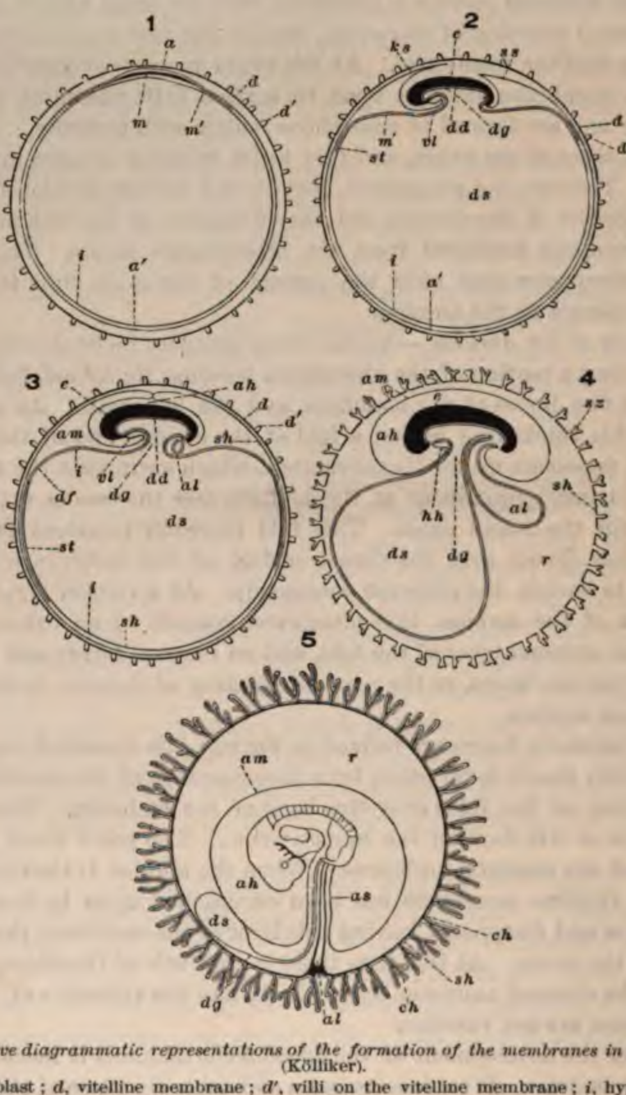


FIG. 295.—*Five diagrammatic representations of the formation of the membranes in the mammalia* (Kölliker).

1: *a*, *a'*, epiblast; *d*, vitelline membrane; *d'*, villi on the vitelline membrane; *i*, hypoblast; *m*, *m'*, mesoblast.

2: *a'*, external layer of the amnion; *d*, *d'*, vitelline membrane; *e*, embryon; *d s*, umbilical vesicle; *v l*, *k s*, *s s*, folds of the amnion; *d d*, *m'*, *s t*, hypoblast; *d d*, connection of the embryon with the umbilical vesicle.

3: *d*, *d'*, vitelline membrane; *v l*, internal amniotic layer; *e*, embryon; *a h*, amniotic cavity; *s h*, *s h*, external amniotic layer; *a m*, space between the two layers of the amnion; *d d*, hypoblast; *d f*, *s t*, *i*, walls of the umbilical vesicle; *d g*, omphalo-mesenteric canal; *d s*, cavity of the umbilical vesicle; *a l*, first appearance of the allantois.

4: *s h*, external layer of the amnion; *s z*, villi of the external layer of the amnion, which has now become the chorion, the vitelline membrane having disappeared; *h h*, *a m*, internal layer of the amnion; *e*, embryon; *a h*, amniotic cavity; *d g*, omphalo-mesenteric canal; *d s*, cavity of the umbilical vesicle; *a l*, allantois; *r*, space between the two layers of the amnion.

5: *c h*, *s h*, *c h*, *a l*, allantois (which has now become the chorion, the external amniotic layer having disappeared), with its villi; *a m*, amnion; *a s*, amniotic covering of the umbilical cord; *r*, space between the amnion and the allantois; *a h*, amniotic cavity; *d s*, umbilical vesicle; *d g*, omphalo-mesenteric canal.

*Plate II.*


FIG. 1.—Human embryon, at the ninth week, removed from the membranes; three times the natural size (Erdl).

FIG. 2.—Human embryon, at the twelfth week, inclosed in the amnion; natural size (Erdl).

cal cord, which connects the embryon with the placental portion of the chorion, and the umbilical vesicle, formed from the same layers as the allantois. 3. The amnion, which is the internal layer of the amniotic fold, persisting throughout fœtal life. 4. The embryon itself.

During the early stages of development of the umbilical vesicle and the allantois, the internal amniotic layer, or the true amniotic membrane, is closely applied to the surface of the embryon, and is continuous with the epidermis, at the umbilicus. It is then separated from the allantois by a layer of gelatinous matter; and in this layer, between the amnion and the allantois, is the umbilical vesicle. At this time the umbilical cord is short and not twisted. As development advances, however, the intermembranous gelatinous matter gradually disappears; the cavity of the amnion is enlarged by the production of a liquid between its internal surface and the embryon; and at about the end of the fourth month, the amnion comes in contact with the internal surface of the chorion. At this time the embryon floats in the amniotic cavity, surrounded by the amniotic fluid.

The amnion forms a lining membrane for the chorion. By its gradual enlargement it has formed a covering for the umbilical cord; and between it and the cord, is the atrophied umbilical vesicle. The amnion then resembles a serous membrane, except that it is non-vascular. It is lined by a single layer of pale, delicate cells of pavement-epithelium, which contain a few fine, fatty granulations. At term the amnion adheres to the chorion, although it may be separated, with a little care, as a distinct membrane and may be stripped from the cord. From its arrangement and from the absence of blood-vessels, it is evident that this membrane is simply for the protection of the fœtus and is not directly concerned in its nutrition and development (see Plate II, Fig. 2). The gelatinous mass referred to above, situated, during the early periods of intraüterine life, between the amnion and the chorion, presents a semi-fluid consistence, with very delicate, interlacing fibres of connective tissue and fine, grayish granulations scattered through its substance. These fibres are gradually developed as the quantity of gelatinous matter diminishes and the amnion approaches the chorion, until finally they form a rather soft, reticulated layer, which is sometimes called the membrana media.

*Amniotic Fluid.*—The process of enlargement of the amnion shows that the amniotic fluid gradually increases in quantity as the development of the fœtus progresses. At term the entire quantity is variable, being rarely more than two pints (about one litre) or less than one pint (about half a litre). In the early periods of utero-gestation it is clear, slightly yellowish or greenish, and perfectly liquid. Toward the sixth month its color is more pronounced and it becomes slightly mucilaginous. Its reaction usually is neutral or faintly alkaline, though sometimes it is feebly acid in the latest periods. It sometimes contains a small quantity of albumen, as determined by heat and nitric acid; and there generally is a gelatinous precipitate on the addition of acetic acid. The following table gives its chemical composition (Robin):

COMPOSITION OF THE AMNIOTIC FLUID.

| | |
|---|---|
| Water | 991·00 to 975·00 |
| Albumen and mucine | 0·82 " 10·77 |
| Urea | 2·00 " 3·50 |
| Creatine and creatinine (Scherer, Robin and Verdeil) | not estimated |
| Sodium lactate (Vogt, Regnauld) | a trace |
| Fatty matters (Rees, Mack) | 0·13 to 1·25 |
| Glucose (Bernard) | not estimated |
| Sodium chloride and potassium chloride | 2·40 to 5·95 |
| Calcium chloride | a trace |
| Sodium carbonate | a trace |
| Sodium sulphate | a trace |
| Potassium sulphate (Rees) | a trace |
| Calcareous and magnesian phosphates and sulphates | 1·14 to 1·72 |

The presence of certain of the urinary constituents in the amniotic fluid has led to the view that the urine of the fœtus is discharged in greater or less quantity into the amniotic cavity. Bernard, who is cited in the table of composition of the amniotic fluid as having determined the presence of sugar, has shown that in animals with a multiple placenta, the amnion has a glycogenic action during the early part of intraüterine existence.

With regard to the origin of the amniotic fluid, it is impossible to say how much of it is derived from the general surface of the fœtus, how much from the urine, and how much from the amnion itself, by transudation from the vascular structures beneath this membrane. The quantity apparently is too great, especially in the early months, to be derived entirely from the urine of the fœtus, and there probably is an exudation from the general surface of the fœtus and from the membranes. After the third month the sebaceous secretion from the skin of the fœtus prevents the absorption of any of the liquid. An important property of the amniotic fluid is that of resisting putrefaction and of preserving dead tissues.

*Formation of the Umbilical Vesicle.*—As the visceral plates, which will be described hereafter, close over the front of the embryon, that portion of the blastoderm from which the intestinal canal is developed presents a vesicle, which is cut off from the abdominal cavity but which still communicates freely with the intestine. This is the umbilical vesicle. On its surface, is a rich plexus of blood-vessels; and this is a very important organ in birds and in many of the lower forms of animals. In the human subject and in mammals, however, the umbilical vesicle is not so important, as nutrition is secured by means of vascular connections between the chorion and the uterus. The vesicle becomes gradually removed farther and farther from the embryon, as development advances, by the elongation of its pedicle, and it is compressed between the amnion and the chorion, as the former membrane becomes distended.

When the umbilical vesicle is formed, it receives two arteries from the two aortæ, and the blood is returned to the embryon, by two veins, which open into the vestibule of the heart. These are called the omphalo-mesenteric vessels. At about the fortieth day one artery and one vein disappear, and soon after, all vascular connection with the embryon is lost. At first there is a canal of communication with the intestine, called the omphalo-mesenteric canal. This is gradually obliterated, and it closes, between the thirtieth and the thirty-fifth day. The point of communication of the vesicle with the intestine is called the intestinal umbilicus; and early in the process of development, there is here a hernia of a loop of intestine. The umbilical vesicle remains as a tolerably prominent structure as late as the fourth or fifth month, but it may often be discovered at the end of pregnancy.

The umbilical vesicle presents three coats; an external, smooth membrane, formed of connective tissue, a middle layer of transparent, polyhedric cells, and an internal layer of spheroidal cells. The membrane, composed of these layers, encloses a pulpy mass, composed of a liquid containing cells and yellowish granulations.

*Formation of the Allantois and the Permanent Chorion.*—During the early stages of development of the umbilical vesicle, and as it is shut off from the intestine, there appears an elevation at the posterior portion of the intestine, which rapidly increases in extent, until it forms a membrane of two layers, which is situated between the internal and the external layers of the amnion. This membrane becomes vascular early in the progress of its development, increases in size quite rapidly, and finally it completely encloses the internal layer of the amnion and the embryon, the gelatinous mass already described being situated between it and the internal amniotic layer before this membrane becomes enlarged. While the formation of the two layers of the allantois is quite distinct in certain of the lower forms of animals, in the human subject and in mammals it is not so easily observed; still there can be no doubt as to the mechanism of its formation, even in the human ovum. Here, however, the allantois soon becomes a single membrane, the two original layers of which can not be separated from each other. The process of the development of the allantois is shown in the diagrammatic Fig. 295 (3, 4, 5).

It is the vascularity of the allantois which causes the rapid development by which it invades and finally supersedes the external layer of the amnion, becoming the permanent chorion, or external membrane of the ovum. At first there are two arteries extending into this membrane from the lower portion of the aorta, and two veins. The two arteries persist and form the two arteries of the umbilical cord, coming from the internal iliac arteries of the fœtus; and one vein, the umbilical vein, which returns the blood from the placenta to the fœtus, is permanent. These vessels are connected with the permanent, vascular tufts of the chorion.

The development of the allantois can not be well observed in human ova before the fifteenth or the twenty-fifth day. When the allantois becomes the permanent chorion, it is marked by a large number of hollow, branching villi over its entire surface, which give the ovum a shaggy appearance. As the ovum enlarges, over a certain area surrounding the point of attachment of the pedicle which connects the chorion with the embryon, the villi are developed more rapidly than over the rest of the surface. Indeed, as the ovum becomes larger and larger, the villi of the surface outside of this area become more and more scanty, lose their vascularity and finally disappear. That portion of the allantois upon which the villi persist and increase in length and in the number of their branches is destined to form connections with the mucous membrane of the uterus and constitutes the fœtal portion of the placenta. This change begins at about the end of the second month, and the placenta becomes distinctly limited at about the end of the third month.

FIG. 296.—*Human embryon at the third week, showing villi covering the entire chorion* (Haeckel).

It must be remembered that as the changes go on which result in the formation of the permanent chorion and the limitation of the fœtal portion of the placenta, the formation of the umbilical vesicle and the enlargement of the amnion are also progressing. The amnion is gradually distended by the increase in the quantity of amniotic fluid. It reaches the internal surface of the chorion at about the end of the fourth month, extends over the umbilical cord to form its external covering, including the cord of the umbilical vesicle, and the umbilical vesicle itself lies in the gelatinous matter between the two membranes.

At about the beginning of the fifth month the ovum is constituted as follows:

The fœtus floats freely in the amniotic fluid, attached to the placenta by the umbilical cord; the chorion presents a highly vascular, thickened and villous portion, the fœtal portion of the placenta; the rest of the chorion is a simple membrane, without villi and without blood-vessels; the amnion lines the internal surface of the chorion and also forms the external covering of the umbilical cord; the umbilical vesicle has become atrophied and has lost its vascularity; the hernia at the point of connection of the umbilical vesicle with the intestine of the fœtus has closed; and finally the fœtus has undergone considerable development.

*Umbilical Cord.*—From the description given of the mode of development of the chorion and the amnion, it is evident that the umbilical cord is nothing more than the pedicle which connects the embryon with that portion of the chorion which enters into the structure of the placenta. It is, indeed, a process of the allantois, in which the vessels eventually become the most important structures. The cord is distinct at about the end of the first month; and as development advances, the vessels consist of two arteries coming from the body of the fœtus, which are twisted usually from left to right, around the single umbilical vein. In addition to the spiral turns of the arteries around the vein, the entire cord may be more or less twisted, probably from the movements of the fœtus.

The fully developed cord extends from the umbilicus of the fœtus to the central portion of the placenta, in which its insertion usually is oblique; although it may be inserted at other points, and even outside of the border of the placenta, its vessels penetrating this organ from the side. Its usual length, which varies very considerably, is about twenty inches (50·8 centimetres). It has been observed as long as sixty (152·4 centimetres), and as short as seven inches (17·8 centimetres). When the cord is very long, it sometimes presents knots, or it may be wound around the neck, the body or any of the members of the fœtus; and this can be accounted for only by the movements of the fœtus in utero.

The external covering of the cord is a process of the amnion; and as it extends over the vessels, it includes a gelatinous substance (the gelatine of Wharton) which surrounds the vessels and protects them from compression. This gelatinous substance is identical with the so-called membrana intermedia, or the substance included between the amnion and the chorion. The entire cord, covered with the gelatine of Wharton and the amnion, usually is about the size of the little finger. According to Robin, the umbilical cord will sustain a weight of about twelve pounds (5·4 kilos). As the amniotic fluid accumulates and distends the amniotic membrane, this membrane becomes more and more closely applied to the cord. The pressure extends from the placental attachment of the cord toward the fœtus, and it gradually forces into the abdomen of the fœtus the loop of intestine, which, in the early periods of intraüterine life, forms an umbilical hernia.

The vessels of the cord, the arteries as well as the vein, are provided with valves. These are simple inversions of the walls of the vessels, and they do not exist in pairs nor do they seem to influence the current of blood. In the arteries these folds are situated at intervals of half an inch to two inches (12·7 to 58·8 mm.), and they are more abundant where the vessels are very contorted. In the vein the folds are most abundant near the placenta. They are very irregularly placed, and in a length of four inches (10 centimetres), fifteen folds were found (Berger). It is not apparent that these valvular folds have any physiological importance.

As the allantois is developed, it presents, in the early stages of its formations, three portions; an external portion, which becomes the chorion, an internal portion, enclosed in the body of the embryon, and an intermediate portion. The intermediate portion becomes the umbilical cord. As the umbilicus of the fœtus closes around the cord, it shuts off a portion of the allantois, contained in the abdominal cavity, which becomes the urinary bladder; but there is a temporary communication between the internal portion and the lower portion of the cord, called the urachus. This generally is obliterated before birth and is reduced to the condition of an impervious cord; but it may persist during intraüterine life, in the form of a narrow canal extending from the bladder to the umbilicus, which is closed soon after birth.

*Membranæ Deciduæ.*—In addition to the two membranes connected with the fœtus, there are two membranes formed from the mucous membrane of the uterus, which are derived from the mother and which serve still farther to protect the ovum. The chorion is for the protection of the fœtus; but a portion of this membrane—about one-third of its surface—becomes closely united with a corresponding portion of the uterine mucous membrane, to form the placenta.

As the fecundated ovum descends into the uterus, it is invested with a shaggy covering, which is either the permanent chorion or one of the membranes which invests the ovum previous to the complete development of the allantois. At this time the mucous membrane of the uterus has undergone certain changes by which it is prepared for the reception of the ovum. The changes which this membrane undergoes in menstruation have already been described. It has been seen that during an ordinary menstrual period, the membrane is increased three or four times in thickness and becomes more or less rugous. If a fecundated ovum descend into the uterus, the changes in the mucous membrane progress. The glands enlarge and the mucous membrane becomes thicker, so that at the end of the first month it measures about two-fifths of an inch (10 mm.). This thickening is due chiefly to development of tissue between the glands, and the membrane becomes soft and pulpy. In the mean time the ovum has effected a lodgement between the folds, usually at the fundus, near the opening of one of the Fallopian tubes; and the adjacent parts of the mucous membrane extend over the ovum so that it is at last completely enclosed. This occurs at the twelfth or thirteenth day (Reichert). The extension of the mucous membrane which covers the ovum becomes the decidua reflexa; the changed mucous membrane which lines the uterus becomes the decidua vera; and the portion of the mucous membrane which remains at the site of the placenta becomes the decidua serotina. The vascular villosities of the chorion do not, as was once thought, penetrate the uterine tubules, but they become surrounded by tissues developed between these tubules.

As development advances, the decidua vera becomes extended, loses its vessels and glands and is reduced to the condition of a simple membrane. The cylindrical epithelium of the mucous membrane of the body of the uterus, soon after fecundation, becomes exfoliated, and its place is supplied by flattened cells. This change is effected at the sixth or the eighth week. The epithelium of the cervix retains its cylindrical character, but most of the cells lose their cilia. The decidua reflexa, which is thinner than the decidua vera, has neither blood-vessels, glands nor epithelium.

During the first periods of utero-gestation, the two layers of decidua are separated by a small quantity of an albuminous and sometimes a sanguinolent fluid; but this disappears at about the end of the fourth month, and the membranes then come in contact with each other. They soon become so closely adherent as to form a single membrane, which is in contact with the chorion. Sometimes, at full term, the membranes of the fœtus can be separated from the decidua; but frequently all of the different layers are closely adherent to each other.

The changes just described are not participated in by the mucous membrane of the neck of the uterus. The glands in this situation secrete a semi-solid, transparent, viscid mucus, which closes the os and is sometimes called the uterine plug.

Toward the fourth month a very delicate, soft, homogeneous layer appears over the muscular fibres of the uterus, beneath the decidua vera, which is the beginning of a new mucous membrane. This is developed very gradually, and the membrane is completely restored about two months after parturition.

*Formation of the Placenta.*—At about the end of the second month the villi of the chorion become enlarged and arborescent over that part which eventually forms the fœtal portion of the placenta. They are then highly vascular and are embedded in the soft substance of the hypertrophied mucous

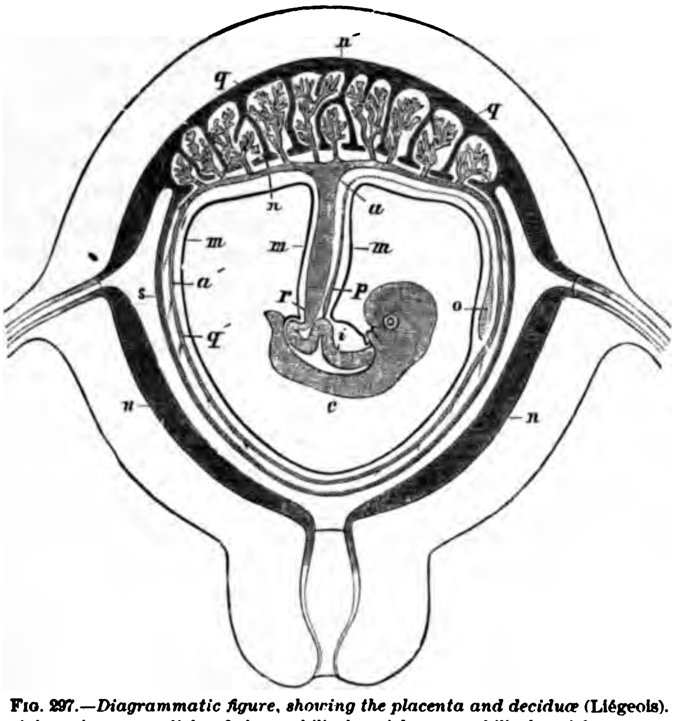


FIG. 297.—*Diagrammatic figure, showing the placenta and deciduæ* (Liégeois).
*c*, embryon ; *i*, intestine ; *p*, pedicle of the umbilical vesicle ; *o*, umbilical vesicle ; *m*, *m*, *m*, amnion ; *a'*, chorion ; *a*, lower end of the umbilical cord ; *q*, *q*, vascular tufts of the chorion, constituting the fœtal portion of the placenta ; *n'*, *n*, maternal portion of the placenta ; *n*, *n*, decidua vera ; *s*, decidua reflexa.

membrane. At the same time the villi over the rest of the chorion are arrested in their growth, and they finally disappear during the third month. The blood-vessels penetrate the villi in the form of loops at about the fourth week; and the placenta is distinctly marked at about the end of the third month. The placenta then rapidly assumes the anatomical characters observed after it may be said to be fully developed.

The fully formed placenta occupies about one-third of the uterine mucous membrane, and generally is rounded or ovoid in form, with a distinct border connected with the decidua and the chorion. It is seven to nine inches (18 to 23 centimetres) in diameter, a little more than an inch (2·5 centimetres) in thickness at the point of penetration of the umbilical cord, slightly attenuated toward the border, and weighs fifteen to thirty ounces (425 to 850 grammes). Its fœtal surface is covered with the smooth, amniotic membrane, and its uterine surface, when detached, is rough, and divided into irregular lobes, or cotyledons, half an inch to an inch and a half (12·7 to 38·1 mm.) in diameter. Between these lobes, are membranes, called dissepiments, which penetrate into the substance of the organ, frequently as far as the fœtal surface.

Upon the uterine surface of the placenta, is a thin, soft membrane, the decidua serotina. This is composed of amorphous matter, a large number of granulations, and colossal cells with enlarged and multiple nuclei. A portion of this membrane is not thrown off with the placenta in parturition, but processes extend into the placenta and closely surround the fœtal tufts.

The two arteries of the umbilical cord branch upon the fœtal surface of the placenta, beneath the amnion, and finally penetrate the substance of the organ. The branches of the veins, which are about sixteen in number, converge toward the cord and unite to form the umbilical vein. Upon the uterine surface of the placenta are oblique openings of a large number of veins which return the maternal blood to the uterine sinuses. There are also the small, spiral arteries, which pass into the substance of the organ, to supply blood to the maternal portion. These are the "curling arteries," described by John Hunter. If the umbilical arteries be injected, the fluid is returned by the umbilical vein, having passed through the vascular tufts of the fœtal portion of the placenta.

According to Winkler, there are three kinds of fœtal villi: 1. Those which terminate just beneath the chorion, without penetrating the vascular lacunæ. 2. Longer villi, which hang free in the lacunæ. 3. Long, branching villi, which penetrate more deeply into the placenta, some extending as far as its uterine surface.

The great vascular spaces, or lacunæ of the maternal portion of the placenta, present a number of trabeculæ, which extend from the uterine to the fœtal surface; and between these trabeculæ, are exceedingly delicate, transverse and oblique secondary trabecular processes. The blood-vessels of the fœtal tufts are surrounded with a gelatinous, connective-tissue structure, and generally are covered with a layer of nucleated epithelium (Winkler).

The mode of formation of the vascular spaces in the placenta has been a subject of much discussion. The following, however, seems to be the most reasonable view with regard to this question: That portion of the uterine mucous membrane which becomes the maternal portion of the placenta extends from the decidua serotina and surrounds the villi, which are embedded in its substance. As the arborescent villi extend, they encroach upon the blood-vessels of the prolongations from the serotina, which latter become much enlarged and finally form the great vascular spaces traversed by the trabeculæ mentioned above. The cells of the serotina form a layer on the walls of the fœtal vessels, and the gelatinous, connective-tissue coverings of these vessels have the same origin. Thus the most important parts of the placenta are formed by an interlacement of the villi of the chorion with the altered structures of the mucous membrane of the uterus.

In the human subject the maternal and fœtal portions of the placenta are so closely united that they can not be separated from each other. In parturition the curling arteries and the veins on the uterine surface of the placenta are torn off, and the placenta then consists of the parts just described; the torn ends of the vessels attached to the uterus are closed by the contractions of the surrounding muscular fibres; and the blood which is discharged is derived mainly from the placenta itself.

*Uses of the Placenta.*—The placenta is the respiratory, excretory and nutritive organ of the fœtus. Its action as a respiratory organ has already been mentioned in connection with the physiology of respiration. It certainly serves as an organ for the elimination of carbon dioxide, and probably also for other products of excretion. It is the only source of materials for the development and nutrition of the fœtus. It is thought that the cells derived from the serotina elaborate a fluid called uterine milk, which is absorbed by the fœtal tufts. This fluid has been collected from between the fœtal tufts of the placenta of the cow, and has been found to contain fatty matter, albuminous matters and certain salts, but no sugar or caseine (Gamgee). It is not certain, however, that such a fluid exists in the human placenta; although "uterine milk" of the ruminants was mentioned distinctly by Haller, and was alluded to by even earlier writers.

## Development of the Ovum.

The product of generation retains the name of ovum until the form of the body begins to be apparent, when it is called the embryon. At the fourth month, about the time of quickening, it is called the fœtus, a name which it retains during the rest of intraüterine life. The membranes are appendages developed for the purposes of protection and nutrition; and the embryon itself, in the mammalia, is developed from a restricted portion of the layers of cells resulting from the segmentation of the vitellus.

The formation of the blastodermic cells and the appearance of the groove which is subsequently developed into the neural canal have already been described. At this portion of the ovum, there is a thickening of the blastoderm, which then presents three layers, the mesoblast, the thickest and most important, being developed from the opposite surfaces of the epiblast and the hypoblast. The earliest stages of development have been studied almost exclusively in the chick; and it is probable that the appearances here observed nearly represent the earlier processes of development in the human subject.

*Development of the Cavities and Layers of the Trunk, in the Chick.*—As an introduction to a description of the development of special organs in the human subject and in mammals, it will be found very useful to study the first stages of development in the chick, which will give an idea of the arrangement of the different blastodermic layers and the way in which they are developed into the different parts of the trunk, with the mode of formation of the great cavities. The figures by which this description is illustrated are those of Brücke, which were photographed on wood from diagrams made from actual preparations by Seboth. These figures, therefore, can hardly be called diagrammatic.

Fig. 298 shows one of the earliest stages of development in the chick. In this figure, the upper layer of dark cells (B, B) represents the epiblast. The


FIG. 298.

lower layer of dark cells (D, D) represents the hypoblast. The middle layer of lighter cells is the mesoblast, which, toward the periphery, is split into two layers. This figure represents a transverse section. At A, is a transverse section of the groove which is subsequently developed into the canal for the spinal cord. Beneath this groove, is a section of a rounded cord (E), the chorda dorsalis. The openings (G, G) represent the situation of the two aortæ. The other cavities are as yet indistinct in this figure.

Fig. 299 shows the same structures at a more advanced stage of development. The dorsal, or vertebral plates, which bound the furrow (A) in Fig.


FIG. 299.

298, are closed above, and include (A) the neural canal. The chorda dorsalis (E) is separated from the cells surrounding it in Fig. 298. The epiblast (B, B) and the hypoblast (D, D) present certain curves which follow the arrangement of the cells of the mesoblast. By the sides of the boundaries of the neural canal, are two distinct masses of cells (C, C), which are developed into the vertebræ. Outside of these masses of cells, are two smaller collections of cells, afterward developed into the Wolffian bodies. Beneath those two masses, are two large cavities (G, G), the largest cavities shown in

Fig. 299, presenting an irregular form, which are sections of the two primitive aortæ. The two openings (H, H) afterward become the pleuro-peritoneal cavity.

In Fig. 300 the parts are still farther developed. The neural canal is represented (A) nearly the same as in Fig. 299, with the chorda dorsalis (E) just beneath it. A groove, or gutter (D) has been formed in front, which is the groove of the intestinal canal. This remains open at this time and is lined by the hypoblast. Just above D, is a single opening (G), which is formed by the union of the two openings (G, G) in Figs. 298 and 299; and this is the abdominal aorta, which has here become single. The two openings (H, H) represent a section of the pleuro-peritoneal cavity. The outer wall of this cavity is the outer visceral plate, which is developed into the muscular walls of the abdomen. The lower and inner wall is the inner visceral plate, which forms the main portion of the intestinal wall. The outer wall is the outer layer of the mesoblast, and the inner wall is the inner layer of the same membrane. The two round orifices (I, I) are sections of the Wolffian ducts. The space (*b*, *b*) is the amniotic cavity.

FIG. 300.

The figures just described, it must be borne in mind, represent transverse sections of the body of the chick, made through the middle portion of the abdomen. The posterior parts, it is seen, are developed first, the situation of the vertebral column being marked soon after the enclosure of the neural canal, by the vertebral plates; and at about the same time, the two aortæ make their appearance, with the first traces of the pleuro-peritoneal cavity. The next organs in the order of development, after the vascular system, are the Wolffian bodies. The intestinal canal is then a simple groove, and the embryon is entirely open in front. In the farther process of development, the visceral plates advance and close over the abdominal cavity, as the medullary plates have closed over the neural canal. Thus there is formed a closed tube, the intestine, lined by the hypoblast, the walls of the intestine being formed of the inner layer of the mesoblast. This brings the external layer of the mesoblast around the intestine, to form the muscular walls of the abdomen, the cavity (Fig. 300, H, H) being the peritoneal cavity, and the external covering being the epiblast. At this time the Wolffian bodies lie next the spinal column, between the intestine and the abdominal walls, with the single, abdominal aorta situated behind the intestine.

### DEVELOPMENT OF THE SKELETON, MUSCULAR SYSTEM AND SKIN.

*Chorda Dorsalis.*—One of the earliest structures observed in the developing embryon is the chorda dorsalis, or notochord. This is situated beneath the neural canal and extends the entire length of the body. It is formed of a cord of simple cells, and marks the situation of the vertebral column, though it is not itself developed into the vertebræ, which grow around it and encroach upon its substance until it finally disappears. In many mammals the notochord presents a slight enlargement at the cephalic extremity, which extends to the auditory vesicles and it is somewhat diminished in size at the caudal extremity. By the sides of this cord are masses of cells which unite in front of the neural canal and eventually are developed into the vertebræ. These are called the protovertebræ and are shown in Fig. 303 (C, in A and B). Twelve pairs of protovertebræ are shown in Fig. 303, C. In the chick, two pairs are first formed in the upper cervical region, on the second day. They rapidly increase in number, from above downward, until at the fourth day there are twenty-one or twenty-two pairs. They are not formed in the region of the head or at the lowest part of the vertebral column. The vertebræ, as they are developed, are formed of temporary cartilaginous structure, gradually extending around the chorda dorsalis,

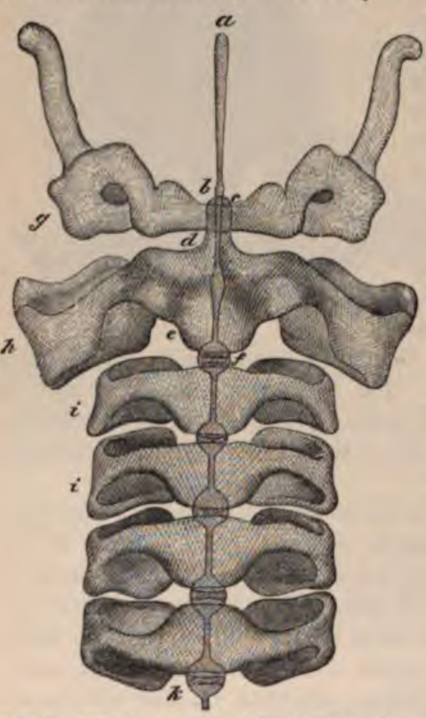


FIG. 301.—*The first six cervical vertebræ of the embryon of a rabbit one inch in length* (Robin).

*a*, *b*, cephalic portion of the notochord, exposed by the removal of the cartilage; *b*, portion of the chorda dorsalis slightly enlarged, which, in this embryon, was situated between the atlas and the occipital bone; *c*, odontoid process; *d*, base of the odontoid process; *e*, inferior, or second part of the body of the axis; *f*, *k*, enlargements of the chorda dorsalis, between the vertebræ; *g*, cartilage of the lateral portion of the atlas; *h*, lateral portion of the axis; *i*, *i*, transverse apophyses of vertebræ.

FIG. 302.—*Human embryon, about one month old, showing the large size of the head and upper parts of the body, the twisted form of the spinal column, the rudimentary condition of the upper and lower extremities and the rudimentary tail at the end of the spinal column* (Dalton).

which then occupies the axis of the spinal column. These cartilages are not divided at the lines of separation of the protovertebræ, but the protovertebræ fuse together and the cartilages which are to be developed into the bodies of the vertebræ are so divided off, that one cartilage occupies the place of the adjacent halves of two protovertebræ. Between the bodies of the vertebræ, the chorda dorsalis presents regular enlargements surrounded by a delicate membrane. As ossification of the spinal column advances, that portion of the chorda dorsalis which is surrounded by the bodies of the vertebræ disappears, leaving the enlargements between the vertebræ distinct. These enlargements, which are not permanent, are gradually invaded by fibrous tissue, their gelatinous contents disappear, and the intervertebral disks, composed of fibro-cartilaginous structure, remain. These disks are permanent between the cervical, the dorsal and the lumbar vertebræ; but they eventually disappear from between the different parts of the sacrum and coccyx, as these are consolidated, this occurring, in the human subject, between the ninth and the twelfth years.

*Vertebral Column, etc.*—In Figs. 299 and 300 (C, C), are seen the two masses of cells (protovertebræ) situated by the sides of the neural canal, which are destined to be developed into the vertebræ. These cells extend around and encroach upon the chorda dorsalis, and form the bodies of the vertebræ. They also extend over the neural canal, closing above, and their processes are called the medullary, or dorsal plates. Sometimes the dorsal plates fail to close at a certain point in the spinal column, and this constitutes the malformation known as spina bifida. From the sides of the bodies of the vertebræ, the various processes of these bones are formed. As the spinal column is developed, its lower portion presents a projection beyond the pelvis, which constitutes a temporary caudal appendage, curved toward the abdomen; but this no longer projects after the bones of the pelvis are fully developed. At the same time the entire vertebral column is curved toward the abdomen, and it is twisted upon its axis, from left to right, so that the anterior face of the pelvis presents a right angle to the upper part of the body; but as the inferior extremities and the pelvis are developed, the spine becomes straight. The vertebræ make their appearance first in the middle of the dorsal region, from which point they rapidly extend upward and downward, until the spinal column is complete.

At the base of the skull, on either side of the superior prolongation of the chorda dorsalis, are two cartilaginous processes, which are developed into the so-called cranial vertebræ. In this cartilaginous mass, three ossific points appear, one behind the other. The posterior point of ossification is for the basilar portion of the occipital bone, which is developed in the same way as one of the vertebræ; the middle point is for the posterior portion of the sphenoid; and the anterior point is for the anterior portion of the sphenoid. The frontal bone, the parietal bone, the temporal bone and a portion of the occipital bone are developed from the connective tissue, without the intervention of pre-existing cartilaginous structure. At the time when the vertebræ are developed, with their laminæ and their spinous and transverse processes, the ribs extend over the thorax, and the clavicle, scapula and sternum make their appearance.

At about the beginning of the second month, four papillary prominences, which are the first traces of the arms and legs, appear on the body of the embryon. These progressively increase in length, the arms appearing near the middle of the embryon, and the legs, at the lower portion. Each extremity is divided into three portions, the arm, forearm and hand, for the upper extremities, and the thigh, leg and foot, for the lower extremities. At the end of each extremity, there are, finally, divisions into the fingers and toes, with the various cartilages and bones of all of these parts, and their articulations.

Very early in intraüterine life the skeleton begins to ossify, from little bony points which appear in the cartilaginous structure. The first points appear at nearly the same time—about the beginning of the second month—in the clavicle and the upper and the lower jaw. Similar ossific points, which gradually extend, are also seen in other parts, the head, ribs, pelvis, scapula, metacarpus and metatarsus, and the phalanges of the fingers and toes. At birth the carpus is entirely cartilaginous, and it does not begin to ossify until the second year. The same is true of the tarsus, except the calcaneum and astragalus, which ossify just before birth. The pisiform bone of the carpus is the last to take on osseous transformation, this occurring between the twelfth and the fifteenth years. As ossification progresses, the deposits in the various ossific points gradually extend until they reach the joints, which remain incrusted with the permanent, articular cartilage.

While the skeleton is thus developing, the muscles are formed from the outer layer of the mesoblast, and the visceral plates close over the thorax and abdomen in front, leaving an opening for the umbilical cord. The various tissues of the external parts, particularly the muscles, begin to be distinct at the end of the second month. The deep layers of the dorsal muscles are the first to be distinguished; then successively, the long muscles of the neck, the anterior straight muscles of the head, the straight and transverse muscles of the abdomen, the muscles of the extremities, the superficial muscles of the back, the oblique muscles of the abdomen and the muscles of the face.

The skin appears at about the beginning of the second month, when it is very delicate and transparent. At the end of the second month the epidermis may be distinguished. The sebaceous follicles are developed at the third month; and at about the fifth month the surface is covered with their secretion mixed with desquamated epithelium. This cheesy substance constitutes the vernix caseosa. At the third month the nails make their appearance, and the hairs begin to grow at about the fifth month. The sudoriparous glands first appear at about the fifth month, by the formation of flask-like processes of the true skin, which are gradually elongated and convoluted, until they are fully developed only a short time before birth.

### Development of the Nervous System.

It has been seen, in studying the development of the spinal column, how the dorsal, or medullary plates close over the groove for the neural canal. In the interior of this canal, the cerebro-spinal axis is developed, by cells which gradually encroach upon its caliber, until there remains only the small, central canal of the spinal cord, communicating with the ventricles of the brain. As the nervous tissue is developed in the interior of the neural canal, there is a separation of the histological elements at the surface, to form the membranes. The dura mater and the pia mater are formed first, appearing at about the end of the second month, while the arachnoid is not distinct until the fifth month. The nerves are not produced as prolongations from the cord into the various tissues nor do they extend from the tissues to the cord, but they are developed in each tissue by a separation of histological elements from the cells of which the parts are originally constituted. The nerves of the sympathetic system are developed in the same way.

The mode of development of the spinal cord is thus sufficiently simple; but with the growth of the embryon dilatations are observed at the superior and at the inferior extremities of the neural canal. The cord is nearly uniform in size in the dorsal region, marked only by the regular enlargements at the sites of origin of the spinal nerves; but there soon appears an ovoid dilatation below, which forms the lumbar enlargement, from which the nerves are given off to the inferior extremities, and the brachial enlargement above, where the nerves of the superior extremities take their origin. At the same time there is a more marked dilatation of the canal at its cephalic extremity. Here a single enlargement appears, which is soon divided into three vesicles, called the anterior, middle and posterior cerebral vesicles. These become more and more distinct as development advances. The formation of these parts is shown in Fig. 303. This figure, in C, shows the projections, on either side, of the vesicles which are eventually developed (*o*, Fig. 303, C) into the nervous portions of the organ of vision.

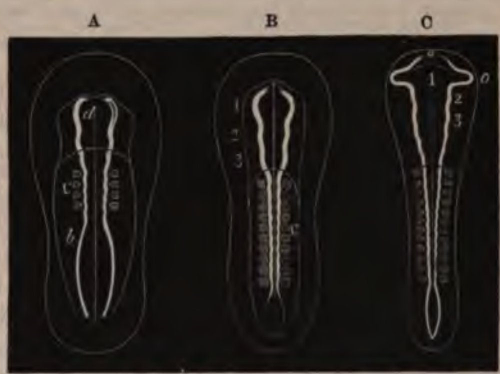


FIG. 303.—*Development of the nervous system of the chick* (Longet, after Wagner).

A, the two primitive halves of the nervous system, twenty-four hours after incubation; B, the same, thirty-six hours after; C, the same, at a more advanced stage. c, the protovertebræ; *b*, posterior dilatation (the lumbar enlargement); *d*, anterior dilatation of the neural canal; 1, 2, 3, anterior, middle and inferior cerebral vesicles; *a*, slight flattening of the anterior cerebral vesicle; *o*, formation of the ocular vesicles.

The three cerebral vesicles now undergo farther changes. The superior, or the first primitive vesicle, is soon divided into two secondary vesicles, the anterior of which becomes the cerebral hemispheres, and the posterior, the optic thalami, which are eventually covered by the greater relative development of the hemispheres. The middle, or second primitive vesicle, does not undergo division and is developed into the tubercula quadrigemina. The posterior, or third primitive vesicle, is divided into two secondary vesicles, the anterior of which becomes the cerebellum, and the posterior, which is covered by the anterior, the medulla oblongata and the pons Varolii. While this division of the primitive cerebral vesicles is going on, the entire chain of encephalic ganglia becomes curved from behind forward, forming three prominent angles. The first of these angles or prominences (*e*, Fig. 304, A, B, C), counting from before backward, is formed by a projection of the tubercula quadrigemina, which at this time constitute the most projecting portion of the encephalic mass; the second prominence (*c*, Fig. 304), situated behind the tubercula quadrigemina, is formed by the projection of the cerebellum; the third (*d*, Fig. 304, A, B, C), is the bend of the superior portion of the spinal cord. These projections and the early formation of certain parts of the encephalon in the human subject are illustrated in Fig. 304.

The cerebrum is developed from the anterior division of the first primitive cerebral vesicle. The development of this part is more rapid in its lateral portions than in the median line, which divides the cerebrum imperfectly into two lateral halves, forming in this way the great longitudinal fissure. At the same time, by the rapid development of the posterior portion, it extends over the optic thalami, the corpora quadrigemina and the cerebellum. Until the end of the fourth month, the hemispheres are smooth on their surface; but they then begin to present large depressions, following folds of the pia mater, which are the first convolutions, these increasing rapidly in number and complexity, especially after the seventh month. The septum lucidum is then formed, by an elevation of nervous matter from the base, which divides the lower portion of the space left between the hemispheres as they ascend, and forms the two lateral ventricles. At the base of these, are developed the corpora striata. The septum lucidum is formed of two laminæ, with a small space between them, which is the cavity of the fifth ventricle. The posterior division of this first primitive vesicle forms the optic thalami. These become separated in front into two lateral halves, but they remain connected together at their posterior portion, which becomes the posterior commissure. The central canal of the cord is prolonged upward between the optic thalami, and forms the third ventricle, which is covered by the hemispheres.


FIG. 304.—*Development of the spinal cord and brain of the human subject* (Longet, after Tiedemann).

A, brain and spinal cord of an embryon of seven weeks; lateral view.

B, the same, from an embryon farther advanced in development; *b*, spinal cord; *d*, enlargement of the spinal cord, with its anterior curvature; *c*, cerebellum; *e*, tubercula quadrigemina; *f*, optic thalamus; *g*, cerebral hemispheres.

C, brain and spinal cord of an embryon of eleven weeks; *b*, spinal cord; *d*, enlargement of the spinal cord, with its anterior curvature; *c*, cerebellum; *e*, tubercula quadrigemina; *g*, cerebral hemispheres; *o*, optic nerve of the left side.

C′, the same parts in a vertical section in the median line, from before backward; *b*, membrane of the spinal cord, turned backward; *d*, second curvature of the upper portion of the spinal cord, which has become thickened and constitutes the peduncles of the cerebrum; *e*, tubercula quadrigemina; *f*, optic thalami, covered by the hemispheres.

The second, or middle cerebral vesicle, becomes filled with medullary substance, extends upward and forms the peduncles of the cerebrum, the upper portion being divided to form the tubercula quadrigemina.

The anterior portion of the third primitive vesicle is developed into the cerebellum, the convolutions of which appear at about the fifth month. Its posterior portion forms the medulla oblongata, in the substance of which is the fourth ventricle, communicating with the third ventricle, by the aqueduct of Sylvius, which is left in the development of the middle vesicle. At about the fourth month there is a deposition of nervous matter in front and above, forming the pons Varolii.

In Fig. 304 (C, *o*), it is seen that the vesicles for the organs of vision appear very early, as lateral offshoots of the anterior cerebral vesicle. These gradually increase in size and advance anteriorly, as development of the other parts progresses. The eyes are situated at first at the sides of the head, gradually approaching the anterior portion. At the extremity of each of these lateral prolongations, a rounded mass appears, which becomes the globe of the eye. The superficial portions of the globe are developed into the sclerotic and the cornea, which seem to be formed of a process from the dura mater. The pedicle attached to the globe becomes the optic nerve. The iris is developed at about the seventh week, and is at first a simple membrane, without any central opening. As the pupil appears, it is closed by a vascular membrane—which probably belongs to the capsule of the crystalline lens—called the pupillary membrane. This membrane gradually disappears, by an atrophy extending from the centre to the periphery. It attains its maximum of development at the sixth month and disappears at the seventh month. The vitreous humor is formed of the fluid contents of the optic vesicle. The crystalline lens is regarded as a product of the epiblast. At the tenth week there is the beginning of the formation of the eyelids. These meet at about the fourth month and adhere together by their edges. In many mammals the eyelids remain closed for a few days after birth; but they become separated in the human subject in the later periods of fœtal life.

It is probable that the vesicle which becomes developed into the internal ear is formed independently; at least cases have been observed in which there was congenital absence of the auditory nerves, the parts of the internal ear being perfect. Soon after the formation of the auditory vesicle, however, it communicates with the third primitive cerebral vesicle, the filament of communication being developed into the auditory nerve.

The auditory vesicle, which appears later than the organ of vision, is eventually developed into the vestibule. The next formations are the arches, or diverticula, which constitute the semicircular canals. The membranous labyrinth appears long before the osseous labyrinth; and it has been found perfectly developed at three months. The bones of the middle ear, which have no connection, in their development, with the nervous system, but which it is convenient to mention here, are remarkable for their early appearance. They appear at the beginning of the third month and are as large in the fœtus at term as in the adult. A remarkable anatomical point with relation to these structures is the existence of a cartilage, attached to the malleus on either side and extending from this bone along the inner surface of the lower jaw, the two cartilages meeting and uniting in the median line, to form a single cord. "This cartilage now ossifies, although, in the commencement, it forms most of the mass of the bone; it disappears at the eighth month" (Meckel). This structure is known as the cartilage of Meckel.

There are no special points for description in the development of the olfactory lobes, which is very simple. These are offshoots from the first cerebral vesicle, appearing at the inferior and anterior part of the cerebral hemispheres, a little later than the parts connected with vision and audition. The vesicles themselves become filled with ganglionic matter and constitute the olfactory bulbs, their pedicles being the so-called olfactory nerves, or olfactory commissures.

As far as the action of the nervous system of the fœtus is concerned, it is probable that it is restricted mainly to reflex phenomena depending upon the spinal cord, and that perception and volition hardly exist. It is probable that many reflex movements take place in utero. When a fœtus is removed from the uterus of an animal, even during the early months of pregnancy, movements of respiration occur; and it is well known that efforts of respiration sometimes take place within the uterus. These are due to the want of oxygen-carrying blood in the medulla oblongata when the placental circulation is interrupted.

## Development of the Digestive Apparatus.

The intestinal canal is the first formation of the digestive system. This is at first open in the greatest part of its extent, presenting, at either extremity of the longitudinal gutter, in front of the spinal column, a rounded, blind extremity, which is closed over in front for a short distance. The closure of the visceral plates then extends laterally and from the two extremities of the intestine, until only the opening remains for the passage of the umbilical cord and the pedicle of the umbilical vesicle. There is at first an open communication between the lower part of the intestinal tube and the allantois, which forms the canal known as the urachus; but that portion of this communication which remains enclosed in the abdominal cavity becomes separated from the urachus, is dilated and eventually forms the urinary bladder. When the bladder is first shut off, it communicates with the lower portion of the intestine, which is called the cloaca; but it finally loses this connection and presents a special opening, the urethra.

Fig. 305.—*Fœtal pig, showing a loop of intestine, forming an umbilical hernia* (Dalton).

From the convexity of the loop, a thin filament is seen passing to the umbilical vesicle, which is here flattened into a leaf-like form.

As development advances, the intestine grows rapidly in length and becomes convoluted. It is held loosely to the spinal column by the mesentery, a fold of the peritoneum, this membrane being reflected along the walls of the abdominal cavity. In the early stages of development, a portion of the intestine protrudes at the umbilicus, where the first intestinal convolution appears; and sometimes there is a congenital hernia of this kind at birth, which usually disappears under the influence of gentle and continued pressure. An illustration of this is given in Fig. 305. This protrusion, in the normal process of development, is gradually returned into the abdomen, as the cavity of the pedicle of the umbilical vesicle is obliterated, at about the tenth week.

At the upper part of the abdominal cavity the alimentary canal presents two lateral projections, or pouches. The one on the left side, as it increases in size, becomes the greater pouch of the stomach, and the one on the right side, the lesser pouch.

At a short distance below the attachment of the pedicle of the umbilical vesicle to the intestine, there appears a rounded diverticulum, which is eventually developed into the cæcum. The cæcum gradually recedes from the neighborhood of the umbilicus, which is its original situation, and finally becomes fixed, by a shortening of the mesentery, in the right iliac region. As the cæcum is developed it presents a conical appendage, which is at first as large as the small intestine and is relatively longer than in the adult. During the fourth week this appendage becomes relatively smaller and more or less twisted, forming the appendix vermiformis. At the second month the cæcum is at the umbilicus, and the large intestine extends in a straight line toward the anus; at the third month it is situated at about the middle of the abdomen; and it gradually descends, until it reaches the right iliac region at about the seventh month. Thus at the second month, there is only a descending colon; the transverse colon is formed at the third month; and the ascending colon, at the fifth month. The ileo-cæcal valve appears at the third month; the rectum, at the fourth month; and the sigmoid flexure of the colon, at the fifth month. During this time the large intestine increases more rapidly in diameter than the small intestine, while the latter develops more rapidly in its length.

In the early stages of development the internal surface of the intestines is smooth; but villi appear upon its mucous membrane during the latter half of intraüterine existence. These are found at first both in the large and the small intestine. At the fourth month they become shorter and less abundant in the large intestine, and they are lost at about the eighth month, when the projections which bound the sacculi of this portion of the intestinal canal make their appearance. The valvulæ conniventes appear, in the form of slightly elevated, transverse folds, in the upper portion of the small intestine. The villi of the small intestine are permanent.

The mesentery is first formed of two perpendicular folds, attached to the sides of the spinal column. As the intestine undergoes development a portion of the peritoneal membrane extends in a quadruple fold from the stomach to the colon, to form the great omentum, which covers the small intestine in front.

As the head undergoes development a large cavity appears, which is eventually bounded by the arches that are destined to form the different parts of the face. This is the pharynx. It is entirely independent, in its formation, of the intestinal canal, the latter terminating in a blind extremity, at the stomach; and between the pharynx and the stomach there is at first no channel of communication. The anterior portion of the pharynx presents, during the sixth week, a large opening, which is afterward partially closed in the formation of the face. The rest of this cavity remains closed until a communication is effected with the œsophagus. The œsophagus appears in the form of a tube, which finally opens into the pharynx above and into the stomach below. At this time there is really no thoracic cavity, the upper part of the stomach is very near the pharynx, the œsophagus is short, the rudimentary lungs appear by its sides and the heart lies just in front. As the thorax is developed, however, the œsophagus becomes longer, the lungs increase in size, and finally the diaphragm shuts off its cavity from the cavity of the abdomen. The growth of the diaphragm is from its periphery to the central portion, which latter gives passage to the vessels and the œsophagus. When this closure is incomplete there is the malformation known as congenital diaphragmatic hernia.

The development of the anus is very simple. At first the intestine terminates below in a blind extremity; but at about the seventh week a longitudinal slit appears below the external organs of generation, by which the rectum opens. This is the anus. It is not very unusual to observe an arrest in the development of this opening, the intestine terminating in a blind extremity, a short distance beneath the integument. This constitutes the malformation known as imperforate anus, a deformity which usually can be relieved, without much difficulty, by a surgical operation, if the distance between the rectum and the skin be not too great. The opening of the anus appears about a week after the opening of the mouth, at or about the seventh week.

The rudiments of the liver appear very early, and, indeed, at the end of the first month this organ has attained a large size. Two projections, or buds, appear on either side of the intestine, which form the two principal lobes of the liver. This organ is at first symmetrical, the two lobes being of nearly the same size, with a median fissure. One of these prolongations from the intestine becomes perforated and forms the excretory duct, of which the gall-bladder, with its duct, is an appendage. During the early part of fœtal life the liver occupies the greatest part of the abdominal cavity. Its weight, in proportion to the weight of the body at different ages, is as follows: At the end of the first month, 1 to 3; at term, 1 to 18; in the adult, 1 to 36 (Burdach). Its structure is very soft during the first months. As development advances and as the relative size of the liver gradually diminishes, its tissue becomes more solid.

The pancreas appears at the left side of the duodenum, by the formation of two ducts leading from the intestine, which branch and develop glandular structure at their extremities. The spleen is developed, about the same time, at the greater curvature of the stomach, and becomes distinct during the second month.

There is no reason to believe that any of the digestive fluids are secreted during intraüterine life. At birth the intestine contains a peculiar substance, called meconium, which will be described farther on. Cholesterine, an important constituent of the bile, is found in large quantity in the meconium.

## Development of the Respiratory System.

On the anterior surface of the membranous tube which becomes the œsophagus, an elevation appears, which soon presents an opening into the œsophagus, the projection forming at this time a single, hollow *cul-de-sac*. This opening becomes the rima glottidis, and the single tube with which it is connected is developed into the trachea. At the lower extremity of this tube, a bifurcation appears, terminating first in one and afterward in several *culs-de-sac*. The bifurcated tube constitutes, after the lungs are developed, the primitive bronchia, at the extremities of which are the branches of the bronchial tree. As the bronchia branch and subdivide, they extend downward into what becomes eventually the cavity of the thorax. The pulmonary vesicles are developed before the trachea (Burdach). The lungs contain no air at any period of intraüterine life and receive but a small quantity of blood; but at birth they become distended with air, are increased thereby in volume and receive all the blood from the right ventricle. This process of development is illustrated in Fig. 306. The lungs appear, in the human embryon, during the sixth week. The two portions into which the original bud is bifurcated constitute the true pulmonary structure, and the formation of the trachea and bronchial tubes occurs afterward and is secondary.

FIG. 306.—*Formation of the bronchial ramifications and of the pulmonary cells.—A, B, development of the lungs, after Rathke; C, D, histological development of the lungs, after J. Müller* (Longet).

## Development of the Face.

The anterior portion of the embryon remains open in front long after the medullary plates have met at the back and enclosed the neural canal. The common cavity of the thorax and abdomen is closed by the growth of the visceral plates, which meet in front. At the time that the visceral plates are closing over the thorax and abdomen, four distinct, tongue-like projections appear, one above the other, by the sides of the neck. These are called the visceral arches, and the slits between them are called the visceral clefts. The first three arches, enumerating them from above downward, correspond, in their origin, to the three primitive cerebral vesicles. The fourth arch—which is not enumerated by some authors, who recognize but three arches—corresponds to the superior cervical vertebræ. Of these four arches, the first is the most important, as its development, in connection with that of the frontal process, forms the face and the malleus and incus of the middle ear. The second arch forms the lesser cornua of the hyoid bone, the stapes and the styloid ligament. The third arch forms the body and the greater cornua of the hyoid. The fourth arch forms the larynx. The first cleft, situated between the first and the second arch, is finally closed in front, but an opening remains by the side, which forms, externally, the external auditory meatus, and internally, the tympanic cavity and the Eustachian tube. The other clefts become obliterated as the arches advance in their development.

From the above sketch, it is seen that the face and the neck are formed by the advance and closure in front of projections from behind, in the same way as the cavities of the thorax and abdomen are closed; but the closure of the first visceral arch is complicated by the projection, from above downward, of the frontal, or intermaxillary process, and by the formation of several secondary projections, which leave certain permanent openings, forming the mouth, nose etc.


FIG. 307.—*Mouth of a human embryon of twenty-five to twenty-eight days; magnified* 15 *diameters* (Coste).

1, median or frontal process, the inferior portion of which is considerably enlarged; 2, right nostril; 3, left nostril; 4, 4, inferior maxillary processes, already united in the median line; 5, 5, superior maxillary processes, which have become quite prominent and have descended to the level of the slope of the frontal process; 6, mouth; 7, first visceral arch; 8, second visceral arch; 9, third visceral arch; 10, eye; 11, ear.

In the very first stages of development of the head there is no appearance of the face. The cephalic extremity consists simply of the cerebral vesicles, the surface of this enlarged portion of the embryon being covered, in front as well as behind, by the epiblast. During the sixth week, after the cavity of the pharynx has appeared, the membrane gives way in front, forming a large opening, which may be called the first opening of the mouth. At this time, however, the face is entirely open in front, as far back as the ears. The first, or the superior visceral arch, now appears as a projection of the mesoblast, extending forward. This is soon marked by two secondary projections, the upper projection forming the superior maxillary portion of the face, and the lower, the inferior maxilla. The two projections which form the lower jaw soon meet in the median line, and their superior margin is the lower lip. At the same time there is a projection from above, extending between the two superior projections, which is called the frontal, or intermaxillary process. This extends from the forehead—that portion which covers the front of the cerebrum—downward. The superior maxillary projections then advance forward, gradually passing to meet the frontal process, but leaving two small openings on either side of the median line, which are the openings of the nostrils. The upper portion of the frontal process thus forms the nose; but below, is the lower end of this process, which is at first split in the median line, projects below the nose, and forms the incisor process, at the lower border of which are finally developed the incisor teeth. As the superior maxillary processes advance forward, the eyes are moved, as it were, from the sides of the head and present anteriorly, until finally their axes become parallel. These processes advance from the two sides, come to the sides of the incisor process, beneath the nose, unite with the incisor process on either side, and their lower margin, with the lower margin of the incisor process, forms the upper lip; but before this, the two lateral halves of the incisor process have united in the median line. At the bottom of the cavity of the mouth a small papilla makes its appearance, which gradually elongates and forms the tongue.

While this process of development of the anterior portion of the first visceral arch is going on, at its posterior portion, the malleus and incus are developing, the former being at first connected with the cartilage of Meckel, which extends along the inner surface of the inferior maxilla, the cartilages from either side meeting at the chin. The cleft between the first and the second visceral arch has closed, except at its posterior portion, where an opening is left for the external auditory meatus, the cavity of the tympanum and the Eustachian tube.

At the same time the second visceral arch advances and forms the stapes, the styloid ligament and the lesser cornua of the hyoid bone. The third arch advances in the same way; and the arches from the two sides meet, become united in the median line and form the body and the greater cornua of the hyoid bone. The clefts between the second and the third and between the third and fourth arches are finally obliterated.

FIG. 308.—*Mouth of a human embryon of thirty-five days* (Coste).

1, frontal process, widely sloped at its inferior portion; 2, 2, incisor processes produced by this sloping; 3, 3, nostrils; 4, lower lip and maxilla, formed by the union of the inferior maxillary processes; 5, 5, superior maxillary processes, contiguous to the incisor process; 6, mouth, still confounded with the nasal fossæ; 7, first appearance of the closure of the nasal fossæ; 8, 8, first appearance of the two halves of the palatine arch; 9, tongue; 10. 10, eyes; 11, 12, 13, visceral arches.

FIG. 309.—*Mouth of an embryon of forty days* (Coste).

1, first appearance of the nose; 2, 2, first appearance of the alæ of the nose; 3, appearance of the closure beneath the nose; 4, middle, or median portion of the upper lip, formed by the approach and union of the two incisor processes, a little notch in the median line still indicating the primitive separation of the two processes; 5, 5, superior maxillary processes, forming the lateral portions of the upper lip; 6, 6, groove for the development of the lachrymal sac and the nasal canal; 7, lower lip; 8, mouth; 9, 9, the two lateral halves of the palatine arch, already nearly approximated to each other in front, but still widely separated behind.

The fourth arch forms the sides of the neck and the larynx, the arytenoid cartilages being developed first. In front of the larynx and just behind the tongue, is a little elevation, which is developed into the epiglottis. The openings of the nostrils appear during the second half of the second month. A little elevation, the nose, appears between these openings, and the nasal cavity begins to be separated from the mouth. The lips are distinct during the third month, and the tongue first appears in the course of the seventh week.

When, by an arrest of development, the superior maxilla on one side fails to unite with the side of the incisor process, there is the very common deformity known as single harelip. If this union fail on both sides, there is double harelip, when the incisor process usually is more or less projecting. As a very rare deformity, it is sometimes observed that the two sides of the incisor process have failed to unite with each other, leaving a fissure in the median line.

The palatine arch is developed by two processes, which arise on either side, from the incisor process, pass backward and upward and finally meet and unite in the median line. The union of these forms the plane of separation between the mouth and the nares; and want of fusion of these processes, from arrest of development, produces the malformation known as cleft palate, in which the fissure is always in the median line. At the same time a vertical process forms in the median line, between the palatine arch and the roof of the nasal cavity, which separates the two nares.

*Development of the Teeth.*—The first appearance of the organs for the development of the teeth is marked by the formation of a cellular projection extending the entire length of the rounded border of either jaw, which forms a rounded band above and dips down somewhat into the subjacent structure. This band is readily separated by maceration, and the removal of the portion that dips into the maxilla leaves a groove. This band extends the entire length of the jaws, without interruption. Its superior surface is rounded, and that portion which dips into the subjacent mucous structure is wedge-shaped, so that its section has the form of a V.

As soon as this primitive band is formed, which occurs at the sixth or seventh week, a flat band projects from its internal surface, near the mucous structure, which is called the epithelial band. This also extends over the entire length of the jaws. It is thin, flattened, with its free edge curved inward and toward the jaw, and is composed at first of a central layer of polygonal cells, covered by a layer of columnar epithelium.

At certain points—these points corresponding to the situation of the true, dental bulbs—there appear rounded enlargements at the free margin of the epithelial band just described. Each one of these is developed into one of the structures of the perfect tooth. The mechanism of the formation of this, which is called the enamel-organ, and of the dental bulb is as follows:

A rounded enlargement appears at the margin of the epithelial band. This soon becomes directed downward—adapting the description to the lower jaw—and dips into the mucous structure, being at first connected with the epithelial band, by a narrow pedicle, which soon disappears, leaving the enlargement enclosed completely in a follicle. This is the dental follicle, and it has no connection with the wedge-shaped band described first. While this process is going on, a conical bulb appears at the bottom of the follicle. The enamel-organ, formed from the epithelial band, becomes excavated, or cup-shaped, at its under surface, and fits over the dental bulb, becoming united to it.

The tooth at this time consists of the dental bulb, with the enamel-organ closely fitted to its projecting surface. The enamel-organ is developed into

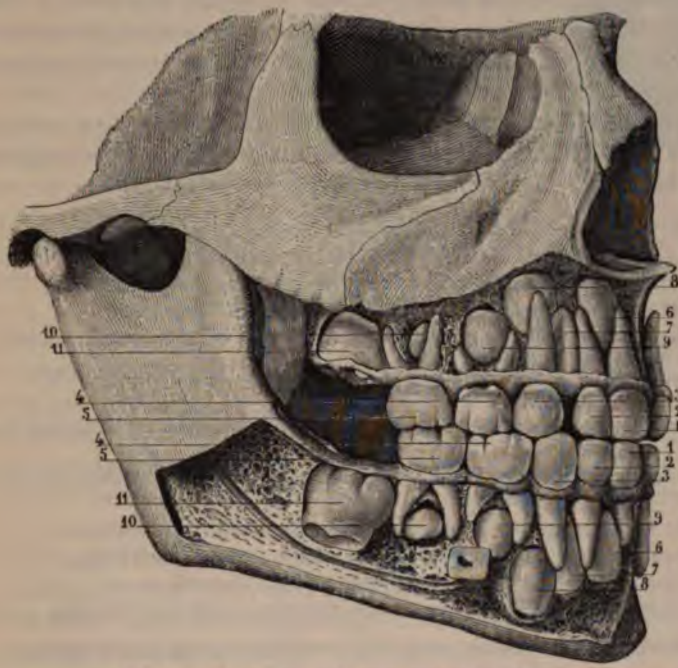

FIG. 310.—*Temporary and permanent teeth* (Sappey).
1, 1, temporary central incisors; 2, 2, temporary lateral incisors; 3, 3, temporary canines; 4, 4, temporary anterior molars; 5, 5, temporary posterior molars; 6, 6, permanent central incisors; 7, 7, permanent lateral incisors; 8, 8, permanent canines; 9, 9, permanent first bicuspids; 10, 10, permanent second bicuspids; 11, 11, first molars.

the enamel; the dental bulb, which is provided with vessels and nerves, becomes the tooth-pulp; and upon the surface of the dental bulb, the dentine is developed in successive layers. The cement is developed by successive layers, upon that portion of the dentine which forms the root of the tooth. As these processes go on, the tooth projects more and more, the upper part of the wall of the follicle gives way and the tooth finally appears at the surface.

The permanent teeth are developed beneath the follicles of the temporary, or milk-teeth. The first appearance is a prolongation or diverticulum from the enamel-organ of the temporary tooth, which dips more deeply into the mucous structure. This becomes the enamel-organ of the permanent tooth; and the successive stages of development of the dental follicles and the dental pulp progress in the same way as in the temporary teeth. As the permanent teeth increase in size, they gradually encroach upon the roots of the temporary teeth. The roots of the latter are absorbed, the permanent teeth advance more and more toward the surface, and the crown of each temporary tooth is finally pushed out. The number of the temporary teeth is twenty, and there are thirty-two permanent teeth. Thus there are three permanent teeth on either side of both jaws, which are developed *de novo* and are not preceded by temporary structures.

The first dental follicles usually appear in regular succession. The follicles for the internal incisors of the lower jaw appear first, this occurring at about the ninth week. All of the follicles for the temporary teeth are completely formed at about the eleventh or twelfth week.

The temporary teeth appear successively, the corresponding teeth appearing a little earlier in the lower jaw. The usual order, subject to certain exceptional variations, is as follows (Sappey):

The four central incisors appear six to eight months after birth.
The four lateral incisors appear seven to twelve months after birth.
The four anterior molars appear twelve to eighteen months after birth.
The four canines appear sixteen to twenty-four months after birth.
The four posterior molars appear twenty-four to thirty-six months after birth.

The order of eruption of the permanent teeth is as follows:

The two central incisors of the lower jaw appear between the sixth and the eighth years.
The two central incisors of the upper jaw appear between the seventh and the eighth years.
The four lateral incisors appear between the eighth and the ninth years.
The four first bicuspids appear between the ninth and the tenth years.
The four canines appear between the tenth and the eleventh years.
The four second bicuspids appear between the twelfth and the thirteenth years.

The above are the permanent teeth which replace the temporary teeth. The permanent teeth which are developed *de novo* appear as follows:

The first molars appear between the sixth and the seventh years.
The second molars appear between the twelfth and the thirteenth years.
The third molars appear between the seventeenth and the twenty-first years.

### Development of the Genito-Urinary Apparatus.

The genital and the urinary organs are developed together and are both preceded by the appearance of two large, symmetrical structures, known as the Wolffian bodies, or the bodies of Oken. These are sometimes called the false, or the primordial kidneys. They appear at about the thirtieth day, develop very rapidly on either side of the spinal column and are so large as to almost fill the cavity of the abdomen. Fig. 311 shows how large these bodies are in the early life of the embryon, at which time their office is undoubtedly very important.

Very soon after the Wolffian bodies have made their appearance, there appear at their inner borders, two ovoid bodies, which are finally developed into the testicles, for the male, or the ovaries, for the female. At their external borders, are two ducts on either side, one of which, the internal, is called the duct of the Wolffian body. This finally disappears in the female, but it is developed into the vas deferens in the male. The other duct, which is external to the duct of the Wolffian body, disappears in the male, but it becomes the Fallopian tube in the female. This is known as the duct of Müller. Behind the Wolffian bodies, are developed the kidneys and the suprarenal capsules.

FIG. 311.—*Fœtal pig, $\frac{5}{8}$ of an inch (15·9 mm.) long.* From a specimen prepared by Dalton.

1, heart; 2, anterior extremity; 3, posterior extremity; 4, Wolffian body.

The abdominal walls have been cut away, in order to show the position of the Wolffian bodies.

As the development of the Wolffian bodies attains its maximum their structure becomes somewhat complex. From their proper ducts, which are applied directly to their outer borders, tubes make their appearance at right angles to the ducts, which extend into the substance of the bodies and become somewhat convoluted at their extremities. These tubes communicate directly with the ducts, and the ducts themselves open into the lower part of the intestinal canal, opposite to the point of its communication with the allantois. The tubes of the Wolffian bodies are simple, terminating in single, somewhat dilated, blind extremities, are lined with epithelium, and are penetrated at their extremities, by blood-vessels, which form coils or convolutions in their interior. These are undoubtedly organs of depuration for the embryon and take on the office to be afterward assumed by the kidneys; but in the female they are temporary structures, disappearing as development advances, and having nothing to do with the development of the true, urinary organs.

The testicles or ovaries are developed at the internal and anterior surface of the Wolffian bodies, first appearing in the form of small, ovoid masses. Beginning just above and passing along the external borders of the Wolffian bodies, are the tubes called the ducts of Müller. These at first open into the intestine, near the point of entrance of the Wolffian ducts. In the female their upper extremities remain free, except the single fimbria which is connected with the ovary. Their inferior extremities unite with each other, and at their point of union they form the uterus. When this union is incomplete there is the malformation known as double uterus, which may be associated with a double vagina. The Wolffian bodies and their ducts disappear, in the female, at about the fiftieth day. A portion of their structure, however, persists in the form of a collection of closed tubes constituting the parovarium, or organ of Rosenmüller.

In the female the ovaries pass down no farther than the pelvic cavity; but the testicles, which are at first in the abdomen of the male, finally descend into the scrotum. As the testicles descend they carry with them the Wolffian duct, that portion of the Wolffian body which is permanent constituting the head of the epididymis. At the same time a cord appears, attached to the lower extremity of the testicle and extending to the symphysis pubis. This is called the gubernaculum testis. It is at first muscular, but the muscular fibres disappear during the later periods of utero-gestation. It is not known that its muscular structure takes any part, by contractile action, in the descent of the testicle in the human subject. The epididymis and the vas deferens are formed from the Wolffian body and the Wolffian duct.

At about the end of the seventh month the testicle has reached the internal abdominal ring; and at this time a double tubular process of peritoneum, covered with a few fibres from the lower portion of the internal oblique muscle of the abdomen, gradually extends into the scrotum. The testicle descends, following this process of peritoneum, which latter become eventually the visceral and parietal portions of the tunica vaginalis. The canal of communication between the abdominal cavity and the cavity of the scrotum is finally closed, and the tunica vaginalis is separated from the peritoneum. The fibres derived from the internal oblique constitute the cremaster muscle.

At the eighth or the ninth month the testicles have reached the external abdominal ring and then soon descend into the scrotum. The vas deferens passes from the testicle, along the base of the bladder, to open into the prostatic portion of the urethra; and as development advances, two sacculated diverticula from these tubes make their appearance, which are attached to the bladder and constitute the vesiculæ seminales.

As the ovaries descend to their permanent situation in the pelvic cavity, there appears, attached to the inner extremity of each, a rounded cord, analogous to the gubernaculum testis. A portion of this, connecting the ovary with the uterus, constitutes the ligament of the ovary; and the inferior portion forms the round ligament of the uterus, which passes through the inguinal canal and is attached to the symphysis pubis.

*Development of the Urinary Apparatus.*—Behind the Wolffian bodies, and developed entirely independently of them, the kidneys, suprarenal capsules and ureters make their appearance. The kidneys are developed in the form of little, rounded bodies, composed of short, blind tubes, all converging toward a single point, which is the hilum. These tubes increase in length, branch, become convoluted in a certain portion of their extent, and they finally assume the structure and arrangement of the renal tubules, with their Malpighian bodies, blood-vessels etc. They all open into the hilum. At the time that the kidneys are undergoing development the suprarenal capsules are formed at their superior extremities. These bodies, the uses of which are unknown, are relatively so much larger in the fœtus than in the adult that they have been supposed to be peculiarly important in intraüterine life, though nothing definite is known upon this point. The kidneys are relatively very large in the fœtus. Their proportion to the weight of the body, in the fœtus, is 1 to 80, and in the adult, 1 to 240. The ureters undoubtedly are developed as tubular processes from the kidneys, which finally extend to open into the bladder. This fact is shown by certain cases of malformation, in which the ureters do not reach the bladder, but terminate in blind extremities. The development of the genito-urinary apparatus can be readily understood, after the discription just given, by a study of Fig. 312.

*Development of the External Organs of Generation.*—The external organs of generation begin to be developed at about the fifth week. At the infe-

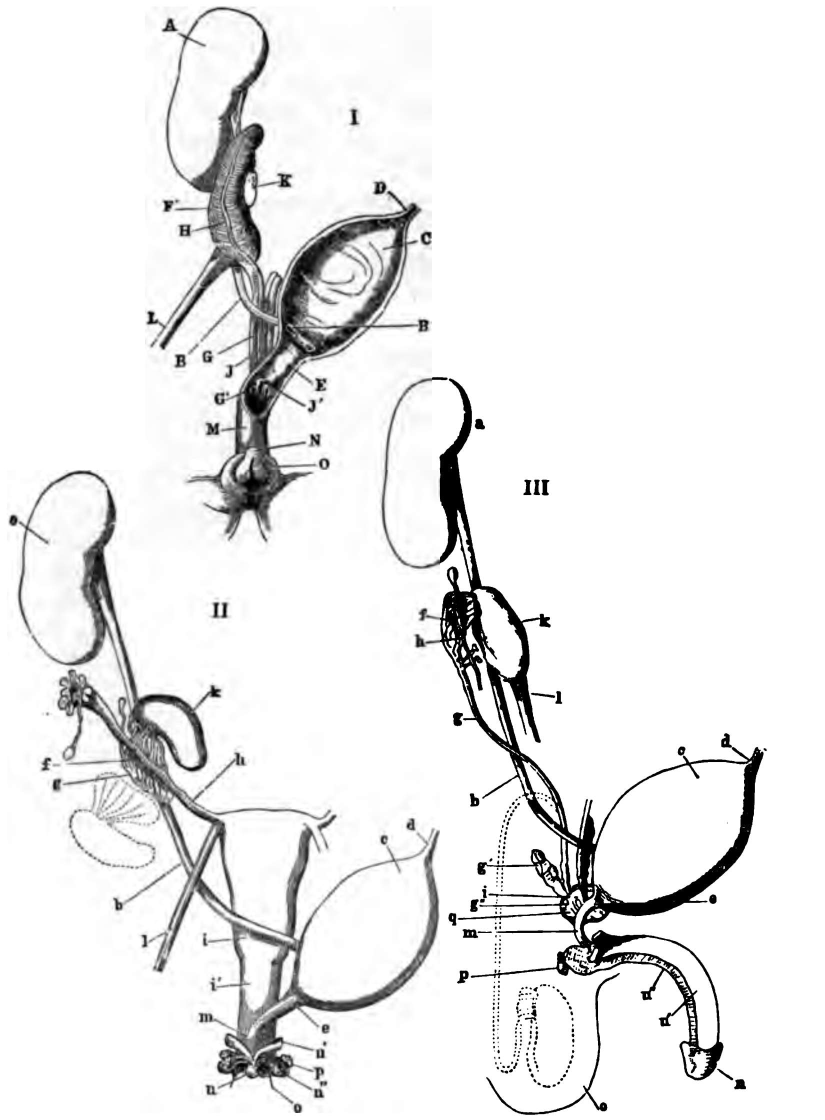

FIG. 312.—*Diagrammatic representation of the genito-urinary apparatus* (Henle).

I, embryonic condition, in which there is no distinction of sex ; II, female form ; III, male form. The dotted lines in II and III represent the situations which the male and female genital organs assume after the descent of the ovaries and testicles. The small letters in II and III correspond to the capital letters in I.

Fig. 312, I.—A, kidney ; B, ureter ; C, bladder ; D, urachus, developed into the median ligament of the bladder ; E, constriction which becomes the urethra ; F', Wolffian body ; G, Wolffian duct, with its opening below, G' ; H, duct of Müller, united below, from the two sides, into a single tube, J, which presents a single opening, J', between the openings of the Wolffian ducts ; K, ovary or testicle ; L, gubernaculum testis or round ligament of the uterus ; M, genito-urinary sinus ; N, O, external genitalia.

Fig. 312, II (female).—a, kidney ; b, ureter ; c, bladder ; d, urachus; e, urethra; f, remains of the Wolffian body (parovarium); g, remnant of the Wolffian duct ; h, Fallopian tube ; i, uterus ; i', vagina ; k, ovary ; l, round ligament of the uterus ; m, extremity of the urethra ; n, clitoris ; n', corpus cavernosum of the clitoris ; n'', bulb of the vestibule ; o, external genital opening ; p, excretory duct of the gland of Bartholinus.

Fig. 312, III (male).—a, kidney ; b, ureter ; c, bladder ; d, urachus ; e, m, urethra ; f, epididymis ; g, vas deferens ; g', seminal vesicle ; g'', ejaculatory duct ; h, i, remains of the duct of Müller ; k, testicle; l, gubernaculum testis ; n, n', n'', urethra and penis ; o, scrotum ; p, gland of Cowper ; q, prostate.

rior extremity of the body of the embryon a small, ovoid eminence appears in the median line, at the lower portion of which there is a longitudinal slit, which forms the common opening of the anus and the genital and urinary passages. This is the cloaca. There is soon developed internally a septum, which separates the rectum from the vagina, the urethra of the female opening above. In the male this septum is developed between the rectum and the urethra, the generative and the urinary passages opening together. From this median prominence two lateral, rounded bodies make their appearance. These are developed, with the median elevation, into the glans penis and corpora cavernosa of the male or into the clitoris and the labia minora of the female. In the male these two lateral prominences unite in the median line and enclose the spongy portion of the urethra. When there is a want of union in the cavernous bodies in the male, there is the malformation known as hypospadias. In the female there is no union in the median line, and an opening remains between the two labia minora. The scrotum in the male is analogous to the labia majora of the female; the distinction being that the two sides of the scrotum unite in the median line, while the labia majora remain permanently separated. This analogy is farther illustrated by the anatomy of inguinal hernia, in which the intestine descends into the labium, in the female, and into the scrotum, in the male. It sometimes occurs, also, that the ovaries descend, very much as the testicles pass down in the male, and pass through the external abdominal ring.

### Development of the Circulatory Apparatus.

The blood and the blood-vessels are developed very early in the life of the ovum and make their appearance nearly as soon as the primitive trace. The mode of development of the first vessels differs from that of vessels formed later, as they appear *de novo* in the blastodermic layers, while afterward, vessels are formed as prolongations of pre-existing tubes. Soon after the epiblast and the hypoblast have become separated from each other and the mesoblast has been formed at the thickened portion of the ovum, which is destined to be developed into the embryon, certain of the blastodermic cells undergo a transformation into blood-corpuscles. These are larger than the blood-corpuscles of the adult and generally are nucleated. At about the same time—it may be before or after the appearance of the corpuscles, for this point is undetermined—certain of the blastodermic cells fuse with each other and arrange themselves so as to form vessels. Leucocytes probably are developed in the same way as the red corpuscles. The vessels thus formed constitute the area vasculosa, which is the beginning of what is known as the first circulation.

According to His and Waldeyer, the cells of the mesoblast do not take part in the formation of the blood and blood-vessels, as indicated above, but cells penetrate at the edges, between the epiblast and the hypoblast, and these, which are called parablastic cells, are developed into blood-vessels and blood-corpuscles. The connective tissue is also supposed to be developed from parablastic cells. According to this view—which, however, is not generally adopted—the parablastic cells are to be distinguished from the cells of the mesoblast, which latter are called archiblastic cells. According to Rindfleisch the so-called parablastic cells are derived from the area opaca.

*The First, or Vitelline Circulation.*—In the development of oviparous animals, the first, or vitelline circulation is very important; for by these vessels the contents of the nutritive yelk are taken up and carried to the em-

FIG. 313.—*Area vasculosa* (Bischoff).
*a*, *a*, *b*, sinus terminalis; *c*, omphalo-mesenteric vein; *d*, heart; *e*, *f*, *f*, posterior vertebral arteries.

bryon, constituting the only source of material for its nutrition and growth. In mammals, however, nutritive matter is absorbed almostly exclusive from the mother, by simple endosmosis, before the placental circulation is established, and by the placental vessels, at a later period. The vitelline circulation is therefore not important, and the vessels dissappear with the atrophy of the umbilical vesicle.

The area vasculosa in mammals consists of vessels coming from the body of the embryon, forming a nearly circular plexus in the substance of the vitellus, around the embryon. The vessels of this plexus open into a sinus at the border of the area, called the sinus terminalis.

In examining the ovum when the area vasculosa is first formed, the embryon is seen lying in the direction of the diameter of the nearly circular plexus of blood-vessels. The plexus surrounds the embryon, except at the cephalic extremity, where the terminal sinuses of the two sides curve downward toward the head, to empty into the omphalo-mesenteric veins. As the umbilical vesicle is separated from the body of the embryon, it carries the plexus of vessels of the area vasculosa with it, the vessels of communication with the embryon being the omphalo-mesenteric arteries and veins. As these processes are going on, the great, central vessel of the embryon becomes enlarged and twisted upon itself, at a point just below the cephalic enlargement of the embryon, between the inferior extremity of the pharynx and the superior *cul-de-sac* of the intestinal canal. The excavation which receives this vessel is called the fovea cardiaca. Simple, undulatory movements take place in the heart of the chick at about the middle of the second day; but there is not at that time any regular circulation. At the end of the second day or the beginning of the third, the currents of the circulation are established. The time of the first appearance of the circulation in the human embryon has not been accurately determined.

In the arrangement of the vessels for the first circulation in the embryon, the heart is situated exactly in the median line and gives off two arches which curve to either side and unite into a single central trunk at the spinal column below. These are the two aortæ, and the single trunk formed by their union becomes the abdominal aorta. The two aortic arches, only one of which is permanent, are sometimes called the inferior vertebral arteries. These vessels give off a number of branches, which pass into the area vasculosa. Two of these branches, however, are larger than the others, pass to the umbilical vesicle and are called the omphalo-mesenteric arteries. In the embryon of mammals, there are at first four omphalo-mesenteric veins, two superior, which are the larger, and two inferior; but as development advances, the two inferior veins are closed, and there are then two omphalo-mesenteric arteries and two omphalo-mesenteric veins. At about the fortieth day one artery and one vein disappear, leaving one omphalo-mesenteric artery and one vein. Soon after, as the circulation becomes established in the allantois, the vessels of the umbilical vesicle and the omphalo-mesenteric vessels are obliterated, and the first circulation is superseded by the second.

As the septum between the two ventricles makes its appearance, that division of the right aortic arch which constitutes the vascular portion of one of the branchial arches disappears and loses its connection with the abdominal aorta; a branch, however, persists during the whole of intraüterine life and constitutes the ductus arteriosus, and another branch is permanent, forming the pulmonary artery.

*The Second, or Placental Circulation.*—As the omphalo-mesenteric vessels disappear and as the allantois is developed to form the chorion, two vessels (the hypogastric arteries) are given off, first from the abdominal aorta; but afterward, as the vessels going to the lower extremities are developed, the branching of the abdominal aorta is such that the vessels become connected with the internal iliac arteries. The hypogastric arteries pass to the chorion, through the umbilical cord, and constitute the two umbilical arteries. At first there are two umbilical veins; but one of them afterward disappears, and there is finally but one vein in the umbilical cord. It is in this way—the umbilical arteries carrying the blood to the tufts of the fœtal placenta, which is returned by the umbilical vein—that the placental circulation is established.

Corresponding to the four visceral arches, which have been described in connection with the development of the face, are four vascular arches. One of these disappears, and the remaining three undergo certain changes, by which they are converted into the vessels going to the head and the superior extremities. The anterior arches on the two sides are converted into the carotids and subclavians; the second, on the left side, is converted into the permanent aorta, and the right is obliterated; the third, on either side, is converted into the right and left pulmonary arteries.

FIG. 314. — *Transformation of the system of aortic arches into permanent arterial trunks, in the mammalia* (Von Baer).

B, aortic bulb: 1, 2, 3, 4, 5, on either side, the five pairs of aortic arches; 5, 5, the earliest in their appearance; 1, 1, the most recent; *c*, *c*, the two carotids, still united, which are separated at a later period; *s*, *s*, the two subclavians, the right arising from the arteria innominata; *a*, *a*, the aorta; *p*, *p*, the pulmonary arteries; *ca*, the ductus arteriosus; *cd*, the left artieral canal, which is finally obliterated.

The changes of the branchial arches are illustrated in the diagrammatic Fig. 314. In this figure the three branchial arches that remain and participate in the development of the upper portion of the vascular system are 1, 2, 3, on either side. The two anterior (3, 3) become the carotids (*c*, *c*) and the subclavians (*s*, *s*). The second (2, 2) is obliterated on the right side, and becomes the arch of the aorta on the left side. The third (1, 1), counting from above downward, is converted into the pulmonary arteries of the two sides. Upon the left side there is a large, anastomosing vessel (*ca*), between the pulmonary artery of that side and the arch of the aorta, which is the ductus arteriosus. The anastomosing vessel (*cd*), between the right pulmonary artery and the aorta, is obliterated.

The mode of development of the veins is very simple. Two venous trunks make their appearance by the sides of the spinal column, which are called the cardinal veins, and run parallel with the superior vertebral arteries, or the two aortæ, emptying finally into the auricular portion of the heart, by two canals, which are called the canals of Cuvier. These veins change their relations and connections as the first circulation is replaced by the second. The omphalo-mesenteric vein opens into the heart, between the two canals of Cuvier. As development advances, the liver is formed in the course of this vessel, a short distance below the heart, and the vein ramifies in its substance; so that the blood of the omphalo-mesenteric vein passes through the liver before it goes to the heart. The omphalo-mesenteric vein is obliterated as the umbilical vein makes its appearance. The blood from the umbilical vein is at first emptied directly into the heart; but this vessel soon establishes the same relations with the liver as the omphalo-mesenteric vein, and its blood passes through the liver before it reaches the central organ of the circulation. As the omphalo-mesenteric vein atrophies, the mesenteric vein, bringing the blood from the intestinal canal, is developed, and this penetrates the liver, becoming finally the portal vein.

As the lower extremities are developed, the inferior vena cava makes its appearance, between the two inferior cardinal veins. This vessel receives an anastomosing branch from the umbilical vein, before it penetrates the liver, and this branch is the ductus venosus. As the inferior vena cava increases in size, it communicates below with the two inferior cardinal veins; and that portion of the two inferior cardinal veins which remains constitutes the two iliac veins. The inferior cardinal veins, between that portion which forms the iliac veins and the heart, finally become the right and the left azygos veins.

The right canal of Cuvier, as the upper extremities are developed, enlarges and becomes the vena cava descendens, receiving finally all the blood from the head and the superior extremities. The left canal of Cuvier undergoes atrophy and disappears. The upper portion of the superior cardinal veins is developed into the jugulars and subclavians on the two sides. As the lower portion of the left cardinal vein and the left canal of Cuvier atrophy, a venous trunk appears, connecting the left subclavian with the right canal of Cuvier. This increases in size and becomes the left vena innominata, which connects the left subclavian and internal jugular with the vena cava descendens.

*Development of the Heart.*—The central enlargement of the vascular system in the first circulation, which becomes the heart, is twisted upon itself by a single turn. The portion connected with the cephalic extremity of the embryon gives origin to the arterial system, and the portion connected with the caudal extremity receives the blood from the venous system. The walls of the arterial portion of the heart soon become thickened, while the walls of the venous portion remain comparatively thin. There then appears a constriction, which partly separates the auricular from the ventricular portion. At a certain period of development the heart presents a single auricle and a single ventricle.

The division of the heart into two ventricles appears before the two auricles are separated. This is effected by a septum, which gradually extends from the apex of the heart upward toward the auricular portion. At the seventh week there is a large opening between the two ventricles. This gradually closes from below upward, the heart becomes more pointed, and the separation of the two ventricles is complete at about the end of the second month.

At about the end of the second month a septum begins to be formed between the auricles. This extends from the base of the heart, toward the ventricles, but it leaves an opening between the two sides—the foramen ovale, or the foramen of Botal—which persists during the whole of fœtal life. At the anterior edge of the opening of the vena cava ascendens into the right auricle, there is a membranous fold, which projects into the auricle. This is the valve of Eustachius, and it divides the right auricle incompletely into two portions.

During the sixth week the heart is vertical and is situated in the median line, with the aorta arising from the centre of its base. At the end of the second month it is raised up by the development of the liver, and its point presents forward. During the fourth month it is twisted slightly upon its axis, and the point presents to the left. At this time the auricular portion is larger than the ventricles; but the auricles diminish in their relative capacity during the latter half of intraüterine life. The pericardium makes its appearance during the ninth week.

Early in intraüterine life the relative size of the heart is very great. At the second month its weight, in proportion to the weight of the body, is as 1 to 50. This proportion, however, gradually diminishes, until at birth the ratio is as 1 to 120. The weight in the adult is about as 1 to 160. During about the first half of intraüterine life the thickness of the two ventricles is nearly the same; but after that time the relative thickness of the left ventricle gradually increases.

*Peculiarities of the Fœtal Circulation.*—Beginning at the abdominal aorta, the blood passes into the two primitive iliacs, and thence into the internal iliacs. From the two internal iliacs the two hypogastric arteries arise, which ascend along the sides of the bladder, to its fundus, pass to the umbilicus and go to the placenta, forming the two umbilical arteries. In this way the blood of the fœtus goes to the placenta.

The umbilical vein enters the body of the fœtus at the umbilicus; it passes along the margin of the suspensory ligament, to the under surface of the liver; it gives off one branch of large size, and one or two smaller branches to the left lobe; it sends a branch each to the lobus quadratus and the lobus Spigelii; and the vessel reaches the transverse fissure. At the transverse fissure it divides into two branches, the larger of which joins the portal vein and enters the liver; and the smaller, which is the ductus venosus, passes to the vena cava ascendens, at the point where it receives the left hepatic vein. Thus the greater part of the blood returned to the fœtus from the placenta passes through the liver, a relatively small quantity being emptied into the vena cava, by the ductus venosus.

The vena cava ascendens, containing the placental blood which has passed through the liver, the blood conveyed directly from the umbilical vein by the ductus venosus and the blood from the lower extremities, passes to the right auricle. As the blood enters the right auricle it is directed by the Eustachian valve, passing behind the valve, through the foramen ovale, into the left auricle. At the same time the blood from the head and the superior extremities passes down, by the vena cava descendens, in front of the Eustachian valve, through the right auricle, into the right ventricle. The arrangement of the Eustachian valve is such that the right auricle simply affords a passage for the two currents of blood; the one, from the vena cava ascendens, through the foramen ovale, passes into the left auricle and the left ventricle; and the other, from the vena cava descendens, passes through the right auriculo-ventricular opening, into the right ventricle. It is probable, indeed, that there is very little admixture of these two currents of blood in the natural course of the fœtal circulation.

The blood poured into the left auricle, from the vena cava ascendens, through the foramen ovale, passes from the left auricle into the left ventricle. The left auricle and the left ventricle also receive a small quantity of blood from the lungs, by the pulmonary veins. Thus the left ventricle is filled. At the same time the right ventricle is filled with blood which has passed

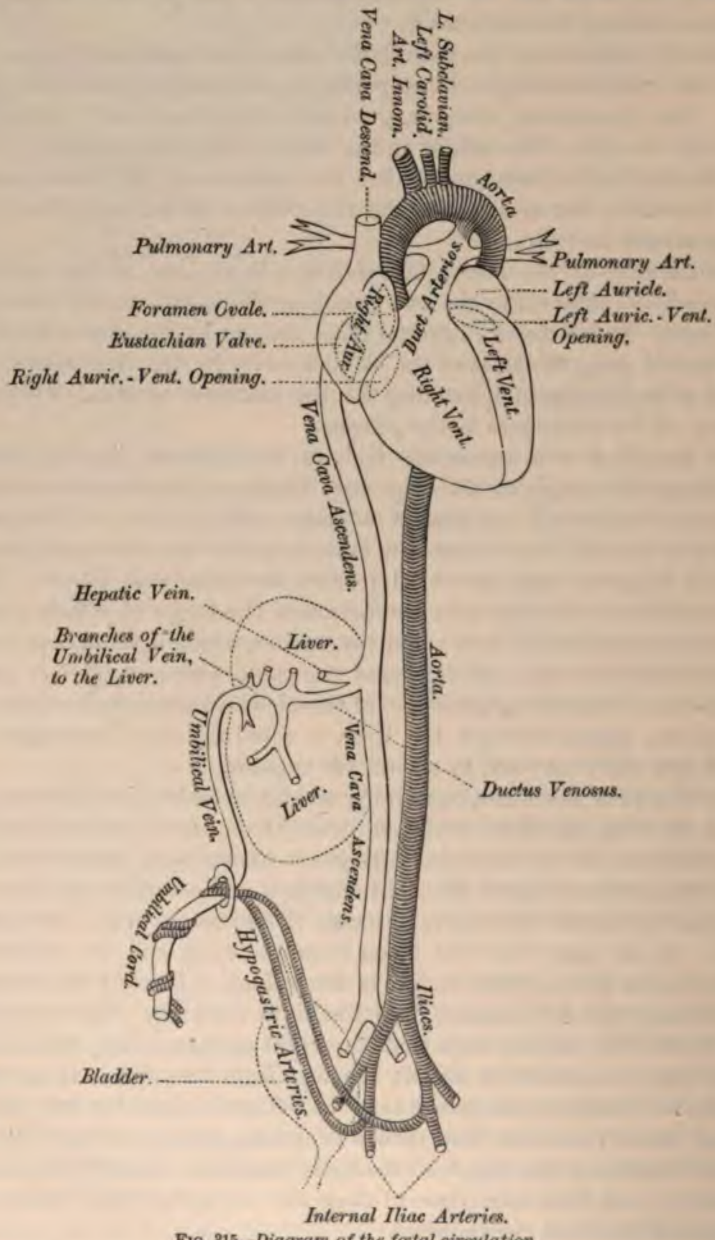

FIG. 315—*Diagram of the fœtal circulation.*

through the right auricle, in front of the Eustachian valve. The two ventricles, thus distended, then contract simultaneously. The blood from the right ventricle passes in small quantity to the lungs, the greater part passing through the ductus arteriosus, into the descending portion of the arch of the aorta. This duct is half an inch (12·7 mm.) in length, and about the size of a goose-quill. The blood from the left ventricle passes into the aorta and goes to the system. The vessels of the head and superior extremities being given off from the aorta before it receives the blood from the ductus arteriosus, these parts receive almost exclusively the pure blood from the vena cava ascendens, the only mixture with the placental blood being the blood from the lower extremities, the blood from the portal system and the small quantity of blood received from the lungs. After the aorta has received the blood from the ductus arteriosus, however, it is mixed blood; and it is this which supplies the trunk and lower extremities.

In Fig. 315, which is diagrammatic, the fœtal circulation is illustrated. In endeavoring, in this figure, to give a clear idea of the second circulation, no attempt has been made to preserve the exact relations or the relative size of the organs. The Eustachian valve, the foramen ovale and the two auriculo-ventricular orifices are represented by dotted lines. The liver and the bladder are also represented by dotted lines.

*The Third, or Adult Circulation.*—When the child is born the placental circulation is suddenly arrested. After a short time the sense of want of air becomes sufficiently intense to give rise to an inspiratory effort, and the first inspiration is made. The pulmonary organs are then for the first time distended with air, the pulmonary arteries carry the greatest part of the blood from the right ventricle to the lungs, and a new circulation is established. During the later periods of fœtal life the heart is gradually prepared for the new currents of blood. The foramen ovale, which is largest at the sixth month, after that time is partly occluded by the gradual growth of a valve, which extends from below upward and from behind forward, upon the side of the left auricle. The Eustachian valve, which is also largest at the sixth month, gradually atrophies after this time, and at full term it has nearly disappeared. At birth, then, the Eustachian valve is practically absent; and after pulmonary respiration becomes established, the foramen ovale has nearly closed. The arrangement of the valve of the foramen ovale is such that at birth a small quantity of blood may pass from the right to the left auricle, but none can pass in the opposite direction. The situation of the Eustachian valve, on the right side of the interauricular septum, is marked by an oval depression, called the fossa ovalis.

As a congenital malformation, the foramen ovale may remain open, producing the condition known as cyanosis neonatorum. This may continue into adult life, and it is then attended with more or less disturbance of respiration and difficulty in maintaining the normal heat of the body. Usually the foramen ovale is completely closed at about the tenth day after birth. The ductus arteriosus begins to contract at birth, and it is occluded, being reduced to the condition of an impervious cord, between the third and the tenth days.

When the placental circulation is arrested at birth, the hypogastric arteries, the umbilical vein and the ductus venosus contract, and they become impervious between the second and the fourth days. The hypogastric arteries remain pervious at their lower portion and constitute the superior vesical arteries. A rounded cord, which is the remnant of the umbilical vein, forms the round ligament of the liver. A slender cord, the remnant of the ductus venosus, is lodged in a fissure of the liver, called the fissure of the ductus venosus.

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## CHAPTER XXVI.

### *FŒTAL LIFE—DEVELOPMENT AFTER BIRTH—DEATH.*

**Enlargement of the uterus in pregnancy—Duration of pregnancy—Size, weight and position of the fœtus—The fœtus at different stages of intrauterine life—Multiple pregnancy—Cause of the first contractions of the uterus, in normal parturition—Involution of the uterus—Meconium—Dextral pre-eminence—Development after birth—Ages—Death—Cadaveric rigidity (rigor mortis).**

As the development of the ovum advances, the uterus is enlarged and its walls are thickened. The form of the organ, also, gradually changes, as well as its position. Immediately after birth its weight is about a pound and a half (680 grammes) while the virgin uterus weighs less than two ounces (56·7 grammes). The neck of the uterus, while it becomes softer and more patulous during pregnancy, does not change its length, even in the very latest periods of utero-gestation (Taylor). The changes in the walls of the uterus during pregnancy are very important. The blood-vessels become much enlarged, and the muscular fibres increase immensely in size, so that their contractions are very powerful when the fœtus is expelled.

It is evident that on account of the progressive increase in the size of the uterus during pregnancy, it can not remain in the cavity of the pelvis during the later months. During the first three months, however, when it is not too large for the pelvis, it sinks back into the hollow of the sacrum, the fundus being directed somewhat backward, with the neck presenting downward, forward and a little to the left. After this time, however, the increased size of the organ causes it to extend into the abdominal cavity, so that its fundus eventually reaches the epigastric region. Its axis then has the general direction of the axis of the superior strait of the pelvis.

The enlargement of the uterus and the necessity of carrying on a greatly increased circulation in its walls during pregnancy are attended with a temporary hypertrophy of the heart. It is mainly the left ventricle which is thickened during utero-gestation, and the increase in the weight of the heart at full term amounts to more than one-fifth. After delivery the weight of the heart soon returns nearly to the normal standard.

*Duration of Pregnancy.*—The duration of pregnancy, dating from a fruitful intercourse, must be considered as variable, within certain limits. The method of calculation most in use by obstetricians is to date from the end of the last menstrual period. Taking into account, however, the various cases which are quoted by authors, in which conception has been supposed to follow a single coitus, there appears to be a range of variation in the duration of pregnancy of not less than 40 days, the extremes being 260 and 300 days. As regards the practical applications of calculations of the probable duration of pregnancy in individual cases, the fact must be recognized that the period is variable. Dating from the end of the last menstrual flow, an average of 278 days, or a little more than nine calendar months, may be adopted.

*Size, Weight and Position of the Fœtus.*—The estimates of writers with regard to the size and weight of the embryon and fœtus at different stages of intraüterine life present very wide variations; still it is important to have an approximate idea, at least, upon these points, and the estimates by Scanzoni are given, as presenting fair averages.

At the third week the embryon is two to three lines (4·2 to 6·4 mm.) in length. This is about the earliest period at which measurements have been taken in the normal state.

At the seventh week the embryon measures about nine lines (19·1 mm.). Points of ossification have appeared in the clavicle and the lower jaw; the Wolffian bodies are large; the pedicle of the umbilical vesicle is very much reduced in size; the internal organs of generation have just appeared; the liver is of large size; the lungs present several lobules.

At the eighth week the embryon is ten to fifteen lines (21·2 to 31·8 mm.) in length. The lungs begin to receive a small quantity of blood from the pulmonary arteries; the external organs of generation have appeared, but it is difficult to determine the sex; the abdominal walls have closed over in front.

At the third month the embryon is two to two and a half inches (50·8 to 63·5 mm.) long and weighs about one ounce (28·3 grammes). The amniotic fluid is then more abundant, in proportion to the size of the embryon, than at any other period; the umbilical cord begins to be twisted; the various glandular organs of the abdomen appear; the pupillary membrane is formed; the limitation of the placenta has become distinct. At this time the upper part of the embryon is relatively much larger than the lower portion.

At the end of the fourth month the embryon becomes the fœtus. It is then four to five inches (10·1 to 12·7 centimetres) long and weighs about five ounces (141·7 grammes). The muscles begin to show contractility; the eyes, mouth and nose are closed; the gall-bladder is just developed; the fontanelles and sutures are wide.

At the fifth month the fœtus is nine to twelve inches (22·8 to 30·5 centimetres) long and weighs five to nine ounces (141·7 to 255·1 grammes). The hairs begin to appear on the head; the liver begins to secrete bile, and the meconium appears in the intestinal canal; the amnion is in contact with the chorion.

At the sixth month the fœtus is eleven to fourteen inches (27·9 to 35·5 centimetres) long and weighs one and a half to two pounds (680 to 907 grammes). If the fœtus be delivered at this time, life may continue for a few moments; the bones of the head are ossified, but the fontanelles and sutures are still wide; the prepuce has appeared; the testicles have not descended.

At the seventh month the fœtus is fourteen to fifteen inches (35·5 to 38·1 centimetres) long and weighs two to three pounds (907 to 1,361 grammes). The hairs are longer and darker; the pupillary membrane disappears, undergoing atrophy from the centre to the periphery; the relative quantity of the amniotic fluid is diminished, and the fœtus is not so free in the cavity of the uterus; the fœtus is now viable.

At the eighth month, the fœtus is fifteen to sixteen inches (38·1 to 40·9 centimetres long and weighs three to four pounds (1,361 to 1,814 grammes). The eyelids are opened and the cornea is transparent; the pupillary membrane has disappeared; the left testicle has descended; the umbilicus is at about the middle of the body, the relative size of the lower extremities having increased.

At the ninth month the fœtus is about seventeen inches (43·2 centimetres) long and weighs five to six pounds (2·27 to 2·72 kilos). Both testicles usually have descended, but the tunica vaginalis still communicates with the peritoneal cavity.

At birth the infant weighs a little more than seven pounds (3·17 kilos), the usual range being between four and ten pounds (1·81 and 4·53 kilos), although these limits are sometimes exceeded.

The position of the fœtus, in the great majority of cases, excluding abnormal presentations, is with the head downward. In the early months of pregnancy the fœtus floats quite freely in the amniotic fluid; and it is probable that the natural gravitation of the head and of the upper part of the fœtus is the determining cause of the ordinary position in utero.

The shape of the uterus at full term is ovoid, the lower portion being the narrower. The fœtus has the head slightly flexed upon the sternum, the arms flexed upon the chest and crossed, the spinal column curved forward, the thighs flexed upon the abdomen, the legs slightly flexed and usually crossed in front, and the feet flexed upon the legs, with their inner margin drawn toward the tibia. This is the position in which the fœtus is best adapted to the size of the uterine cavity, and in which the expulsive force of the uterus can be most favorably exerted, both as regards the fœtus and the generative passages of the mother.

*Multiple Pregnancy.*—It is not very rare to observe two children at a birth, and cases are on record where there have been four and even five, though in these latter instances the children generally survive but a short time, or as is more common, abortion takes place during the first months. Examples of three at a birth have been often observed.

In cases of twins it is an interesting question to determine whether the development always takes place from two ova or whether a single ovum may be developed into two beings. In the majority of cases, twins are of the same sex, though sometimes they are male and female. In some cases there are two full sets of membranes, each fœtus having its distinct decidua, placenta and chorion; in others there is a single chorion and a double amnion; but in some both fœtuses are enclosed in the same amnion. As a rule the two placentæ are distinct; but sometimes there is a vascular communication between them, or what appears to be a single placenta may give origin to two umbilical cords. If there be but a single chorion and amnion and a single placenta, it has been thought that the two beings are developed from a single ovum; otherwise it would be necessary to assume that there were originally two sets of membranes, which had become fused into one. The instances on record of twins, one white and the other black, show conclusively that two ova may be developed in the uterus at the same time. While there can be no doubt upon this point, the question of the possibility of the development of two beings from a single ovum remains unsettled.

As pathological conditions, extraüterine pregnancies occur, in which the fecundated ovum, forming its attachments in the Fallopian tube (Fallopian pregnancy) or within the abdominal cavity (abdominal pregnancy), undergoes a certain degree of development. The uterus usually enlarges in these instances and forms an imperfect decidua.

*Cause of the First Contractions of the Uterus in Normal Parturition.*—The cause of the first contraction of the uterus in normal parturition is undoubtedly referable to some change in the attachment of its contents, which causes the fœtus and its membranes to act as a foreign body. When for any reason it is advisable to cause the uterus to expel its contents before the full term of pregnancy, the most physiological method of bringing on the contractions of this organ is to cautiously separate a portion of the membranes, as is often done by introducing an elastic catheter between the ovum and the uterine wall. A certain time after this operation, the uterus contracts to expel the ovum, which then acts as a foreign body.

In the normal state, toward the end of pregnancy, the cells of the decidua vera and of that portion of the placenta which is attached to the uterus undergo fatty degeneration, and in this way there is a gradual separation of the outer membrane, so that the contents of the uterus gradually lose their anatomical connection with the mother. When this change has progressed to a certain extent, the uterus begins to contract; each contraction then separates the membranes more and more, the most dependent part pressing upon the os internum; and the subsequent contractions are due to reflex action. The first "pain" is induced by the presence of the fœtus and its membranes as a foreign body, a mechanism similar to that which obtains when premature labor has been brought on by separation of the membranes.

According to Körner, there exists in the spinal cord, at the site of the first and second lumbar vertebræ, a reflex centre for parturition. This, like other centres in the cord, is subordinate to a centre which is situated in the medulla oblongata.

The mechanism of parturition, although this is entirely a physiological process, is considered elaborately in works upon obstetrics. The first contractions of the uterus, by pressing the bag of waters against the os internum, gradually dilate the cervix; the membranes usually rupture when the os is pretty fully dilated, and the amniotic fluid is discharged; the head then presses upon the outlet; and the uterine contractions becoming more and more vigorous and efficient, the child is brought into the world, this being followed by the expulsion of the membranes and placenta. There then follows a tonic contraction of the muscular walls of the uterus, which becomes a hard, globular mass, easily felt through the flaccid, abdominal walls. The very contractions of the muscular fibres of the uterus which expel the fœtus close the vessels ruptured by the separation of the placenta and arrest the hæmorrhage from the mother. The changes which then take place in the respiration and the circulation of the infant have been considered in connection with the development of the circulatory system.

*Involution of the Uterus.*—At four to six days, and seldom later than eight days after parturition, the uterus has sensibly advanced in the process of involution; and it is then gradually reduced to the size and structure which it presents during the non-pregnant condition, though it never becomes quite as small as in the virgin state. The new mucous membrane, which has been developing during the latest periods of pregnancy, becomes perfect at about the end of the second month after delivery. It has then united, at the os internum, with the mucous membrane of the neck, which has not participated in the formation of the decidua. The muscular fibres, after parturition, present granules and globules of fat in their substance, and are gradually reduced in size as the uterus becomes smaller. Their involution is complete at about the end of the second month. During the first month, and particularly within the first two weeks after delivery, there is a sero-sanguinolent discharge from the uterus, which is due to disintegration of the blood and of the remains of the membranes in its cavity, this *débris* being mixed with a certain quantity of sero-mucous secretion. This discharge constitutes the lochia. It is at first red but becomes paler as it is reduced in quantity and disappears.

*Meconium.*—At about the fifth month there is a certain quantity of secretion in the intestinal canal, which becomes more abundant, particularly in the large intestine, as development advances. This is rather light-colored or grayish in the upper portion of the small intestine, becoming yellowish in the lower portion, and it is of a dark-greenish color in the colon. The dark, pasty, adhesive matter, which is discharged from the rectum soon after birth, is called the meconium.

The meconium appears to consist of a thick, mucous secretion, with abundant, grayish granules, a few fatty granules, intestinal epithelium, and frequently crystals of cholesterine. The color seems to be due to granulations of the coloring matter of the bile, but the biliary salts can not be detected in the meconium, by Pettenkofer's test. The constituent of the meconium which possesses the greatest physiological importance, is cholesterine. Although but few crystals of cholesterine are found upon microscopical examination, the simplest processes for its extraction will reveal the presence of this substance in large quantity. In a specimen of meconium in which a quantitative examination was made, the proportion of cholesterine was 6·245 parts per 1,000 (Flint). The meconium contains cholesterine and no stercorine, the stercorine, in the adult, resulting from a transformation of cholesterine, by the digestive fluids, which probably are not secreted during intraüterine life.

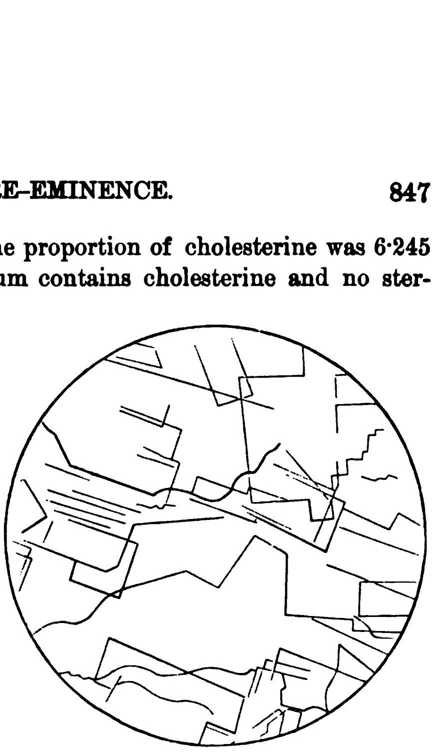

FIG. 816.—*Cholesterine extracted from meconium.*

None of the secretions concerned in digestion appear to be produced in utero, and it is also probable that the true, biliary salts are not formed at that time; but the processes of disassimilation and excretion are then active, and the cholesterine of the meconium is the product of the excretory action of the liver. The relations of cholesterine as an excrementitious product have already been very fully discussed, in connection with the bile and with excretion.

*Dextral Pre-eminence.*—Most persons by preference use the right arm, leg, eye etc., instead of the left; but exceptionally some use the left in preference to the right. There can be no doubt with regard to the fact of a natural, dextral pre-eminence; and also, that left-handedness is congenital, difficult if not impossible to correct entirely, and not due simply to habit. It would appear that there must be some condition of organization, which produces dextral pre-eminence in the great majority of persons, and left-handedness, as an exception; but what this condition is, it is very difficult to determine. An explanation which was offered by anatomists is that the right subclavian artery arises nearer the heart than the left, that the right arm is therefore better supplied with arterial blood, develops more fully, and therefore is generally used in preference to the left; but the exceptional predominance of the left hand can not be explained in this way.

The most important anatomical and pathological facts bearing upon the question under consideration are the following: Boyd has shown that the left side of the brain almost invariably exceeds the right in weight, by about one-eighth of an ounce (3·5 grammes). In aphasia the lesion is almost always on the left side of the brain. These facts point to a predominance of the left side of the brain, which presides over the movements of the right side of the body. Again, a few cases of aphasia with left hemiplegia, the lesion being on the right side of the brain, have been reported as occurring in left-handed persons. Ogle gives several such instances, in which the brain-lesion was on the right side. In two left-handed individuals, the brain was examined and compared with the brain of right-handed persons. It was found that the brain was more complex on the left side in the right-handed, and on the right side, in the left-handed. Bastian has found the gray matter of the brain generally to be heavier on the left than on the right side. With regard to the cause of the superior development of the left side of the brain, the only explanation offered is the fact that the arteries going to the left side usually are larger than those on the right. There are no observations with regard to the comparative size of the arteries upon the two sides in left-handed persons.

Reasoning from the facts just stated, Ogle has assumed that dextral pre-eminence depends upon a natural predominance of the left side of the brain, the reverse obtaining in the left-handed. This view seems to afford the most rational explanation of dextral pre-eminence. Generally it is true that the members on the right side are stronger than the left, particularly the arm; but this is not always the case, even in the right-handed, although the right hand is more conveniently and easily used than the left. In many feats of strength, the left arm appears less powerful than the right, because there is less command over the muscles. As regards the cause of the superior development of the left side of the brain, it must be admitted that the anatomical explanation is not entirely satisfactory. It is a fact, however, that the two sides of the brain generally are not exactly equal in their development, the left side usually being superior to the right, and that the muscles of the right side of the body generally are used in preference to those of the left side.

## Development after Birth, Ages and Death.

When the child is born, the organs of special sense and the intelligence are dull; there is then very little muscular power; and the new being, for several weeks, does little more than eat and sleep. The natural food at this time is the milk of the mother, and the digestive fluids do not for some time possess the varied solvent properties that are found in the adult, though observations upon the secretions of the infant are few and rather unsatisfactory. The full activity of pulmonary respiration is gradually and slowly established. Young animals appropriate a comparatively small quantity of oxygen, and just after birth they present a much greater power of resistance to asphyxia than the adult. The power of maintaining the animal temperature is also much less in the newly-born. The processes of ossification, development of the teeth etc., have already been described. The hairs are shed and replaced by a new growth a short time after birth. The fontanelles gradually diminish in size after birth, and they are completely closed at the age of about four years.

The period of life which dates from birth to the age of two years is called infancy. At the age of two years the transition takes place from infancy to childhood. The child is then able to walk without assistance, the food is more varied and the digestive operations are more complex. The special senses and the intelligence become more acute, and the being begins to learn how to express ideas in language. The child gradually develops, and the milk-teeth are replaced by the permanent teeth. At puberty, which begins between the fourteenth and the seventeenth years—a little earlier in the female—the development of the generative organs is attended with important physical and moral changes.

The different ages recognized by physiologists are the following: Infancy, from birth to the age of five years; adolescence, or youth, to the twenty-fifth year; adult age, to the thirty-fifth year; middle life, to the fiftieth year; old age, to the sixtieth year; and then, extreme old age. A man may be regarded at his maximum of intellectual and physical development at about the age of thirty-five, and he begins to decline after the sixtieth year, although this rule, as regards intellectual vigor, has many exceptions.

As regards nutrition, it may be stated in general terms that the appropriation of new matter is a little superior to disassimilation, to about the age of twenty-five years; between twenty-five and forty-five these two processes are nearly equal; and at a later period the nutrition does not completely supply the physiological waste of the tissues, the proportion of organic to inorganic matter gradually diminishes, and death follows, as an inevitable consequence of life. In old age the muscular movements gradually become feeble; the bones contain an excess of inorganic matter; the ligaments become stiff; the special senses generally are somewhat obtuse; and there is a diminished capacity for mental labor, with more or less loss of memory and of intellectual vigor. It is a curious fact that remote events are more clearly and easily recalled to the mind in old age than those of recent occurrence; and, indeed, early impressions and prejudices then appear to be unusually strong.

It frequently happens in old age that some organ essential to life gives way, and that this is the immediate cause of death, or that an old person is stricken down by some disease to which his age renders him peculiarly liable. It is so infrequent to observe a perfectly physiological life, continuing throughout the successive ages of man, that it is almost impossible to present a picture of physiological death; but it sometimes occurs that there is a gradual fading away of vitality in old persons, who die without being affected with any special disease. It is also difficult to fix the natural period of human life. Some persons die, apparently of old age, at seventy, and it is rare that life is preserved beyond one hundred years. The tissues usually die successively and not simultaneously, nearly all of them being dependent upon the circulating, oxygen-carrying blood, for the maintenance of their physiological properties. It has been demonstrated, indeed, that the properties of tissues may be restored for a time, after apparent death, by the injection of blood into their vessels.

After death there often is a discharge of the contents of the rectum and bladder, and parturition, even, has been known to take place. The appearance which indicates growth of the beard after death is probably due to shrinking of the skin and, perhaps, contraction of the smooth muscular fibres attached to the hair-follicles. The most important phenomenon, however, which is observed before putrefaction begins, is a general rigidity of the muscular system.

*Cadaveric Rigidity* (*Rigor Mortis*).—At a variable time after death, usually five to seven hours, all of the muscles of the body, involuntary as well as voluntary, become rigid, and can be stretched only by the application of considerable force. Sometimes, especially after long-continued and exhausting diseases, this rigidity appears as soon as a quarter of an hour after death. In the case of persons killed suddenly while in full health, it may not be developed until twenty or thirty hours after death, and it then continues for six or seven days. Its average duration is twenty-four to thirty-six hours; and as a rule it is more marked and lasts longer the later it appears. In warm weather cadaveric rigidity appears early and continues for a short time. When the contraction is overcome by force, after the rigidity has been completely established and has continued for some time, it does not reappear. The rigidity of the muscular system extends to the muscular coats of the arteries and lymphatics. During what may be called the first stage the muscles are still excitable; but when the rigidity is complete their excitability is lost and can not be restored. Cadaveric rigidity is always preceded by loss of excitability of the motor nerves.

The rigidity first appears in the muscles which move the lower jaw. Then it is noted in the muscles of the trunk and neck, extends to the arms, and finally to the legs, disappearing in the same order of succession. The stiffening of the muscles is due to a coagulation of their substance, analogous to the coagulation of the blood, and probably is attended with some shortening of the fibres; at all events, the fingers and thumbs generally are flexed. That the rigidity is not due to coagulation of the blood, is shown by the fact that it occurs in animals dead from hæmorrhage.

According to John Hunter the blood does not coagulate nor do the muscles become rigid in animals killed by lightning or hunted to death; but it is a question in these instances whether the rigidity does not begin very soon after death and continue for a brief period, so that it may escape observation. As a rule rigidity is less marked in very old and in very young persons than in the adult. It occurs in paralyzed muscles, provided they have not undergone extensive fatty degeneration.

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# INDEX.

THE END.

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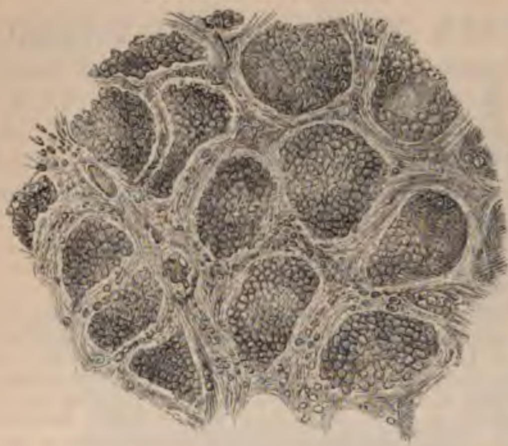

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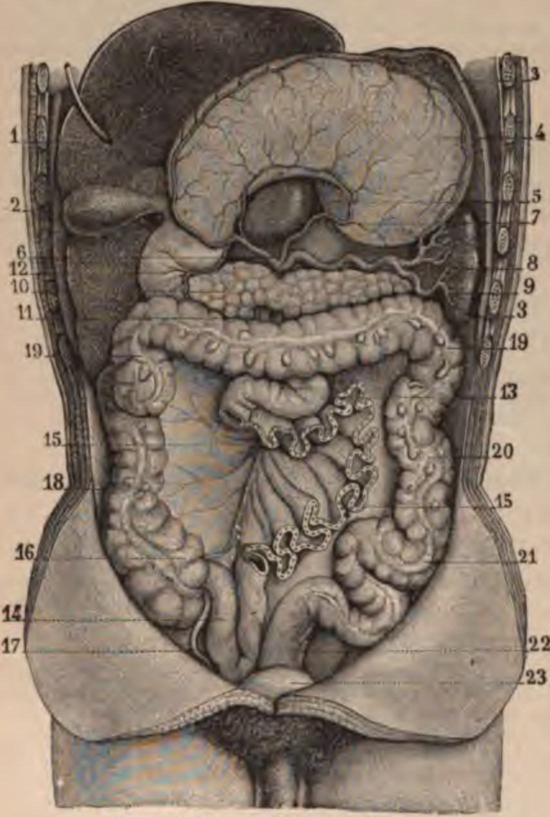

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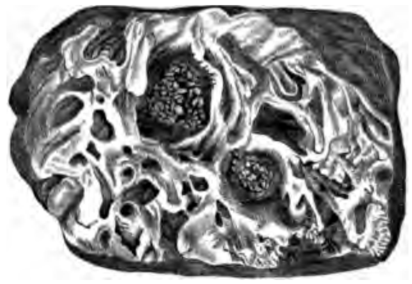

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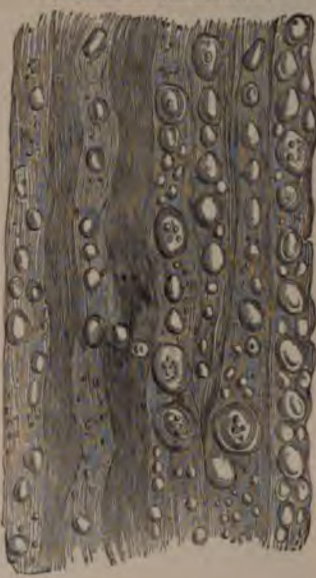

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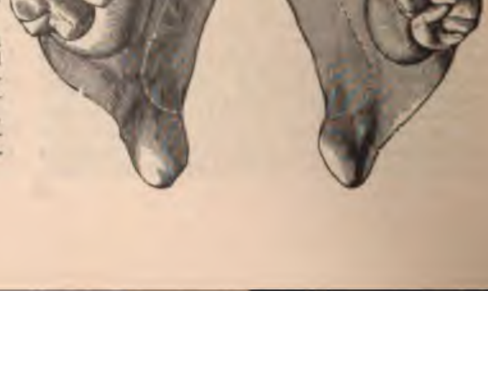

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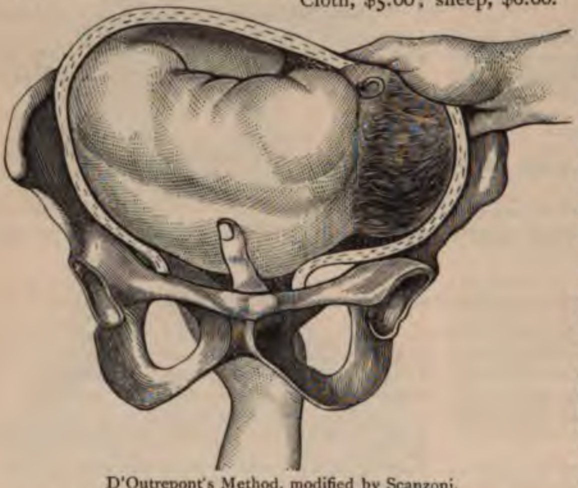

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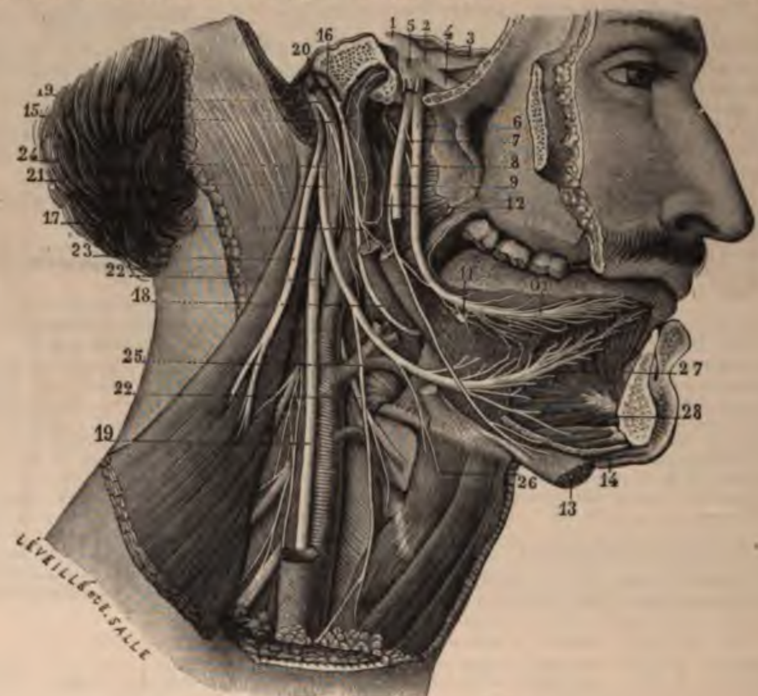


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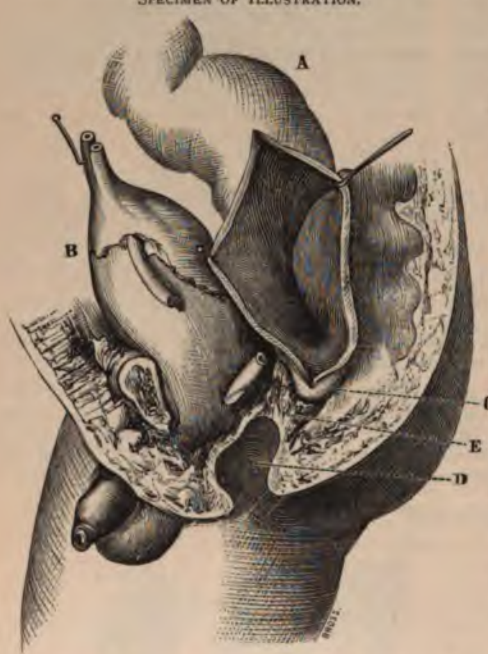


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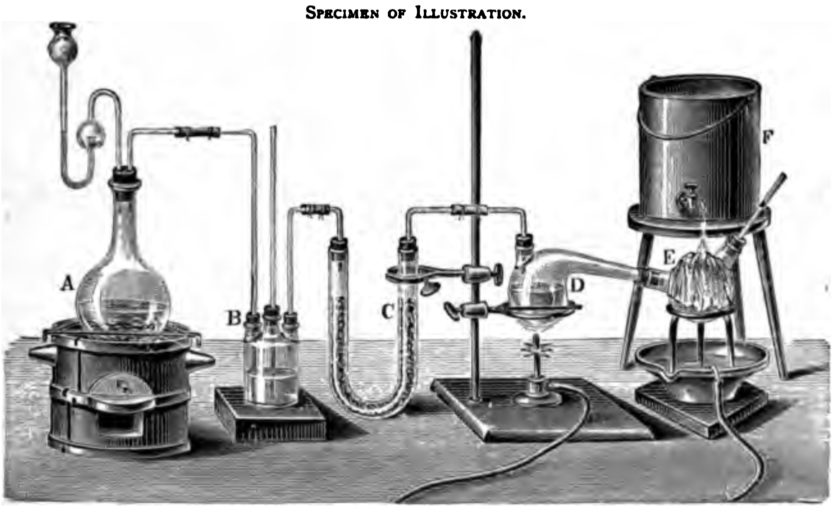


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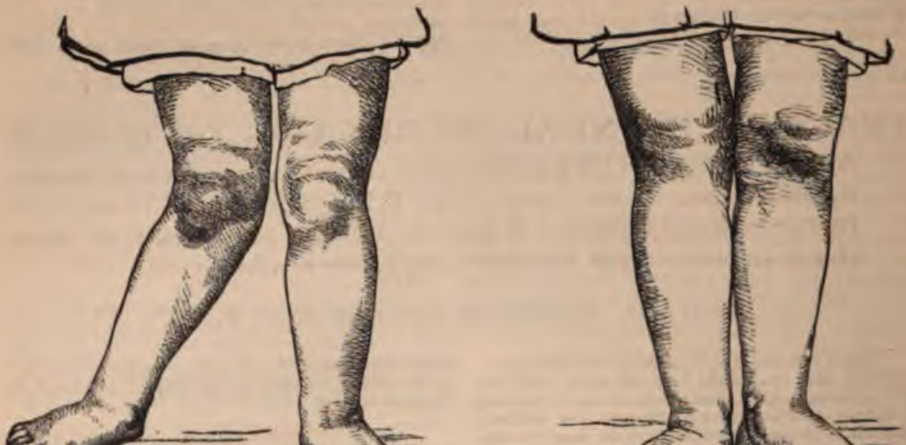

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Fig. 390.—Making Plantar Flap.

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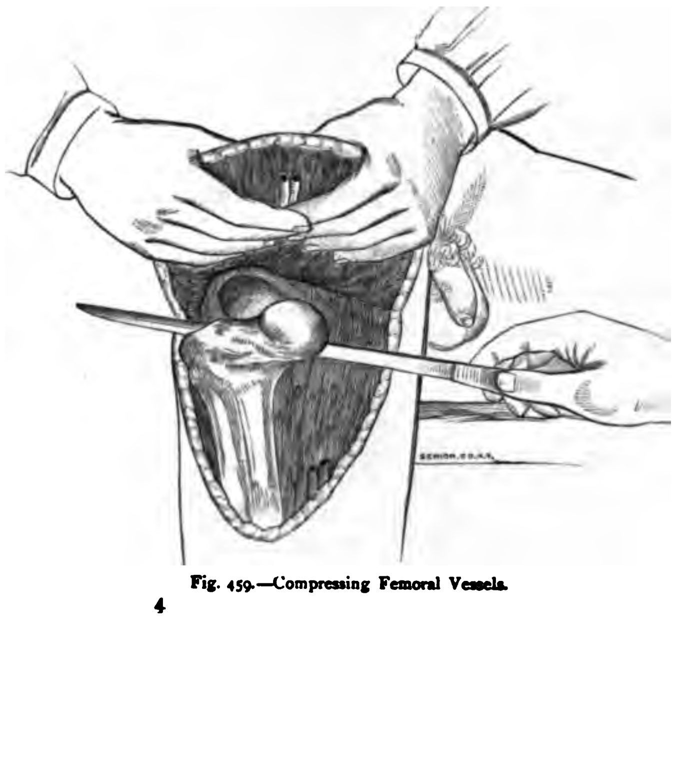

Fig. 459.—Compressing Femoral Vessels.

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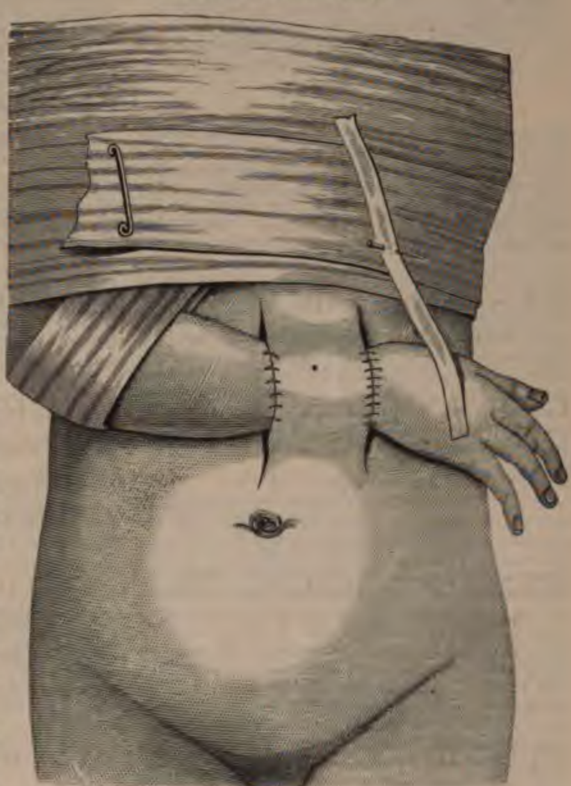

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Fig. 147.—Necrotomy of tibia. Leg placed on a hard cushion. Irrigator playing from the right.

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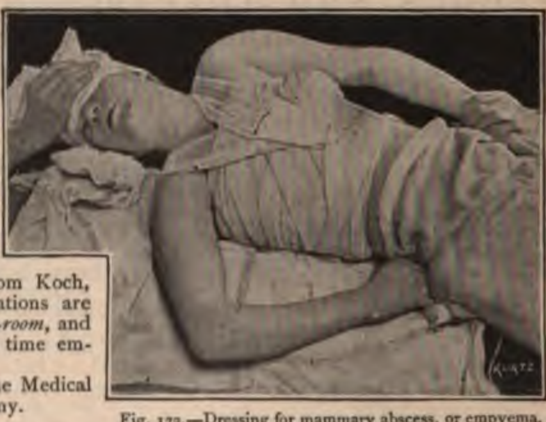

Fig. 172.—Dressing for mammary abscess, or empyema.

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